Feeding Ecology of Cory's Shearwater in the Portuguese Atlantic

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To the memory of my grand-father, for his love, joy and wisdom

To Alexandra, Rita and Marta, for their love

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Abstract

This thesis considers aspects of the morphology, diet and feeding ecology of Cory's shearwater *Calonectris diomedea* in the Portuguese Atlantic (sub-tropical and temperate north east Atlantic). Morphological variability among colonies in measurements of adult Cory's shearwater in the Mediterranean, Atlantic and Cape Verde is described. Discriminant methods are employed to enable identification of each sex from bill measurements, in some Atlantic colonies.

Relationships between the size and weight of several species of prey fish and the dimensions of diagnostic hard structures (vertebrae, otoliths) are presented, to enable back-calculation of size of prey from remains found in diet samples. The importance of using information from all hard remains present in food samples is discussed in the context of biases in dietary studies of piscivorous animals. The diet of Cory's shearwater in the archipelago of the Azores is described, and comparisons are made with the diet of other marine predators occurring in this area. The use of shearwaters as monitors of pelagic environments is briefly discussed. An interspecific study is described to test the existence of a causal relationship linking mercury levels in the plumage of seabirds with the levels found in the organisms that constitute their prey. The implications for the use of seabirds as monitors of mercury contamination are examined.

The patterns of activity and burrow attendance of breeding Cory's shearwaters are analysed, using a novel logging system. The system records data on date, time, identity, of marked birds entering and leaving their nests. Data on the reliability of the system are presented, and its potential use in studies of other burrow-nesting animals is discussed. Existing methods developed to assess the natural patterns of food delivery to nestling Procellariiformes are critically examined, using independent information on parental behaviour provided by the logging system. Some implications of errors in the underlying assumptions of these methods on the understanding of the adaptive significance of reproductive traits of Procellariiformes are discussed. A flexible foraging behaviour of Cory's shearwater in a year of presumed low food availability is documented, and this behaviour is interpreted in relation to a situation of "normal" abundance of food resources. The ability of Cory's shearwaters to adopt alternative long and short foraging trips is discussed in the context of the life-history strategies of long-lived seabirds.

An experimental study testing the influence of the nutritional status of the chicks on the provisioning behaviour of Cory's shearwater is presented. Results are discussed in light of current hypotheses explaining regulation of food delivery in Procellariiformes.

Chapter 1

General Introduction

Seabirds have long been recognised as suitable sampling units for monitoring the marine environment (Cairns 1987, Furness & Monaghan 1987, Furness & Greenwood 1993). In particular, a large amount of research has been directed towards examining the potential use of seabirds as monitors of the condition of commercially important fish stocks (Montevecchi 1993, Furness & Camphuysen 1997). Although based on robust and mathematically sound models, current fishery stock assessment methods can still fail to provide accurate information about condition of target fish stocks or inaccurately predict the development of fish prey populations (Cairns 1992). Therefore, the response of seabirds to changes in the abundance of their prey has received considerable attention, as they could provide independent evidence of stock condition (Montevecchi 1993).

The magnitude and persistence of prey changes to a large extent determine the level and intensity of seabird response (Cairns 1987, 1992, Montevecchi 1993, Furness & Camphuysen 1997). While major depletion of stocks of preferred prey can induce changes in seabird life-table variables (e.g. by directly affecting adult survival or breeding success), more subtle variations in food availability are probably only likely to be detected by minor changes in seabird activity budgets (e.g. feeding frequency, territorial attendance). Ecological aspects of the feeding and foraging of the monitor species should be well understood, if seabirds are to be used effectively to trace fish abundance (Furness & Monaghan 1987).

The effects of changes in food supply will strongly depend on the way each species obtains food at sea. Large differences are expected to arise between species which explore the entire water column such as auks and penguins, and those which have only a limited ability to dive and therefore depend on the availability of prey relatively close to the surface (Furness & Ainley 1984). Similarly, coastal species generally explore highly productive waters on continental shelf areas, but may be severely affected by changes in local stocks, whereas pelagic seabirds, which rely on scarce and patchily distributed organisms, can possibly switch to alternative foraging areas, at relatively low cost (Croxall 1987). Specialised species are likely to exhibit more pronounced responses compared to generalist feeders, and the former will

naturally reflect more accurately changes in abundance of a single prey item (Montevecchi 1993).

Several studies have established causal links between food availability and various types of seabird responses, ranging from total breeding failure (e.g. associated with major collapse of local stocks as caused by the El Niño Southern Oscillation; Schreiber & Schreiber 1984, 1989), to less obvious changes in activity budgets (e.g. Hamer et al. 1991, Klomp & Furness 1992a, Monaghan et al. 1994, Uttley et al. 1994, Phillips et al. 1996). It should be noted that while seabirds can reflect prevailing feeding opportunities, large aggregations in restricted areas will possibly induce noticeable changes in the overall availability of certain prey, by depletion of local food stocks (Furness & Birkhead 1984, Birt et al. 1987, Furness & Monaghan 1987, Monaghan 1992). In these cases, interactions with fishery interests are likely to occur.

In any case, it is very clear that the reliability of the information derived from the behaviour of seabirds will depend to a large extent on a detailed knowledge of their feeding ecology and on the understanding of their role in marine food webs. In response to this need, a vast amount of information is now available on ecological aspects of feeding in seabirds (e.g. Croxall 1987, Springer et al. 1987, Burger 1988), especially around major fishery areas in the Northern hemisphere, such as the North Sea (Furness & Tasker 1997), Barents Sea (Anker-Nilssen et al. 1997) and the Gulf of Alaska (Springer et al. 1986). In the Southern hemisphere, Antarctic and sub-Antarctic waters support large populations of penguins and petrels, and their roles and impact in marine ecosystems are also well documented (Croxall et al. 1984, Croxall 1989, Croxall et al. 1997).

Among seabirds, Procellariiformes consist mainly of species that exploit pelagic food resources. Since few other seabird taxa make extensive use of pelagic habitats, it is from Procellariiformes that we should look for species that could be used as indicators of pelagic prey stocks (Croxall 1989, Cherel & Weimerskirch 1995). Procellariiformes include some of the least studied seabird species, and a few still lack baseline information on breeding biology and population dynamics (Warham 1990, 1996). This Order comprises more than 100 species, only slightly less than Charadriiform seabirds (skuas, gulls, terns, skimmers and auks, Furness &

Monaghan 1987, Warham 1990, 1996). Nonetheless, their extreme life-history strategies have attracted much attention from behavioural and evolutionary ecologists (Wynne-Edwards 1955, Lack 1968, Ashmole 1971, Wooller et al. 1992). Indeed, this group is renowned for their low adult mortality rate, deferred breeding, single-egg clutch and slow chick growth. The high longevity of Procellariiformes (and generally of most seabird species) has discouraged the development and maintenance of long-term studies, but the few existing studies (reviewed by Wooller et al. 1992) have provided an invaluable insight into understanding the evolution of life-history strategies in this group.

David Lack provided the first conceptual framework under which several life-history traits of Procellariiformes were integrated (Lack 1968). In particular, he inferred that reproductive characters of this Order (e.g. slow chick growth and large accumulation of fat during the nestling period), evolved as a response to an unpredictability and scarcity of food resources at sea (Lack 1968). Energetic limitations associated with the transport of food to chicks at the colony were also thought to represent severe constraints for regular provisioning in these seabirds (Ashmole 1971). According to Lack's view "... in the Procellariiformes (...), the nestlings are fed intermittently, and a major function of the fat is probably to tide them over such temporary periods of shortage..." (Lack 1968).

Ricklefs et al. (1985) provided the first of a series of studies critically examining Lack's hypothesis linking food availability to Procellariiform life-history traits. He proposed a methodological approach to test this hypothesis, by analysing the patterns, rates and variability in food delivery to nestling petrels. The method suggested by Ricklefs et al. (1985) was based on periodic weighing of chicks at the nest, as a means of deducing parental behaviour. This indirect approach was particularly appropriate for nocturnal species, and avoided the enormous effort and undue disturbance that a direct observational procedure would represent. According to this methodology, the feeding episodes are ascertained by the magnitude of chick weight increments between (usually nocturnal) weightings. Over a period of one or more nights, the proportion of chicks that did not receive any meal can be used to derive a feeding probability, as P(Fed) = [1-P(not fed)] = [1 - (proportion of chicks

not fed)$^{1/2}$]. In fact, under the assumption of independence of parental visits, the number of chicks fed by one and two adults can be estimated from binomial probabilities. The meals are then assigned to visits by one or by two parents, by considering that the largest meals correspond to double feeds, whereas smaller ones result from delivery by a single adult (Ricklefs et al. 1985).

Over the last 15 years, this procedure was adopted by numerous studies (with minor refinements) as a standard approach, therefore yielding a considerable amount of comparative data (e.g. Klomp & Furness 1992b, Hamer & Hill 1993, Bolton 1995a, Lorentsen 1996, Hamer et al. 1997). Most of the evidence obtained from these studies failed to provide support for Lack's (1968) food unpredictability hypothesis. In fact, there was little evidence of prolonged periods of poor feeding condition, as would be required to justify the magnitude of fat accumulation in nestling Procellariiformes. Furthermore, results obtained from modelling adult behaviour were able to replicate the observed levels of fat accumulation, and yet did not consider severe limitations imposed by scarce food resources at sea (Ricklefs & Schew 1994). These authors suggested that the patterns of food delivery in this group were not influenced by the nutritional state of the chick, but rather would depend on the amount of time the adult would need to achieve a certain threshold of energy. This alternative hypothesis views lipid deposits in nestling petrels as a consequence of stochastic variation in foraging success, affecting each individual adult. Accumulation of fat reserves would not have an adaptive value *per se* but rather would represent a by-product, arising from the tendency of adults to, on average, overfeed their chick to avoid the risks of chance starvation (Ricklefs & Schew 1994).

According to the Ricklefs & Schew (1994) view, the provisioning process in this group is under the strict control of the parents, who regulate the rate of delivery according to an energy-threshold mechanism. Hence, parents are predicted to exhibit a limited ability to respond to the needs of their chick at the nest (Ricklefs & Schew 1994). While recent studies have shown that some species do not respond to short-term requirements of chicks (e.g. Hamer & Hill 1993, Hamer et al. 1997), other have reached opposite conclusions (e.g. Bolton 1995a, Hamer & Thompson 1997). The evidence from experimental studies is also equivocal, and similarly contrasting

responses were obtained (e.g. Hamer & Hill 1994, Ricklefs 1987, 1992 *vs* Bolton 1995b, Weimerskirch et al. 1997).

Surprisingly, no study has yet addressed the implications that violating any of the assumption underlying the method proposed by Ricklefs et al. (1985) could have on the final conclusions. This could be done both by means of modelling the patterns of food delivery by adults and by using alternative or independent methods for resolving adult presence. A lack of independence in parental behaviour has been noticed (e.g. Hamer & Hill 1993), but the effects on the results were not assessed. It is also likely that on some occasions, large single feeds exceed meals delivered by two adults (e.g. Schaffner 1990). Chicks can also fail to accept all the food brought by the parents, as described by Weimerskirch et al. (1997) in albatrosses. The implications of these probably widespread phenomena for studies using Ricklefs et al. (1985) "blind periodic weighing" remains totally unknown. In fact, the efficiency of their method in checking these "deviations" in behaviour is as yet to be verified, and certainly need critical examination. Finally, the data to which this method applies are constituted by repeated measurements, obtained from a limited number of individuals. It is well known that individuals will systematically differ in their ability to provision food to their chick (e.g. Lorentsen 1996). It is therefore not unlikely that individuals respond differently to a trade-off between feeding frequency and amount of food delivery. If this is the case, smaller single feeds would be over-represented in relation to larger ones, as the former are delivered more frequently. Under these circumstances, effects due to pseudo-replication are likely to occur (Hurlbert 1984) and this possibility, although acknowledged, has seldom being correctly accounted for.

Although a large amount of data has been gathered from Procellariiform species at temperate and high latitudes, this contrasts with a paucity of similar information from many tropical and subtropical oceanic areas. At these regions of low-latitude, data on population numbers, breeding biology and feeding ecology are still relatively scant. This is the case in the Portuguese Atlantic, a wide oceanic area, encompassing a sub-tropical sector extending from the Azorean archipelago, south to

Madeira (including the Desertas and Selvagem islands), and north to temperate waters, off the Portuguese coast (Figure 1). All the fieldwork presented in the thesis was carried out in this area.

Fifteen seabird species regularly breed in the Portuguese Atlantic (Table 1) and among these, Procellariiformes assume a particular importance, in terms of number of species (8), population sizes and conservation interest. Indeed, most Procellariiform species are listed as Species of Unfavourable Conservation Status (Tucker & Heath 1994), and the Portuguese Atlantic holds a significant proportion of their European populations (Hagemeijer & Blair 1997).

Cory's shearwater *Calonectris diomedea* is the most abundant seabird in this area (Table 1). Two subspecies are currently recognised (Cramp & Simmons 1977, Hagemeijer & Blair 1997 and references therein): the nominate *C. diomedea diomedea*, breeds in several islands in the Mediterranean, with a breeding population estimated between 50000 and 60000 pairs, distributed from Aegean Sea to the Balearic islands. The Atlantic form, *C. diomedea borealis* occurs in the archipelagos of Azores, Madeira and in the Canary islands. It also breeds in small numbers on Berlenga island, about 10 km off the Portuguese coast. In the Atlantic, the currently estimated breeding population is 80000–130000 pairs (Hagemeijer & Blair 1997), although it further includes an unknown but certainly very large number of non-breeding birds. Several aspects of their breeding biology and population dynamics have been described (Zino 1971, Mougin et al. 1984, Granadeiro 1991, Mougin et al. 1997).

Life-history theory predicts that the investment in a breeding episode should be decided in relation to prospects of future reproductive investment (Stearns 1992). The life-history traits exhibited by seabirds suggest severe constraints imposed by the limited availability of food resources (Lack 1968, Ashmole 1971, Weimerskirch et al. 1997). Among seabirds, Procellariiformes strongly rely on pelagic prey, which are scarce, dispersed and so unpredictable in location. These characteristics of prey distribution in the oceanic environment confers a high variability in foraging success of petrels. Under these circumstances, albatroses, shearwaters and storm petrels represent very suitable group to address hypothesis related to reproductive effort,

Table 1 - Current breeding estimates of seabird populations in the Portuguese Atlantic (updated from Monteiro et al. 1995). Values refer to number of breeding pairs.

Species	Portugal (mainland)	Azores (3)	Madeira and Porto Santo	Desertas	Selvagens	Total
Madeira's petrel *Pterodroma madeira*	-	-	20 - 30 (1)	-	-	20 - 30
Fea's petrel *Pterodroma feae*	-	-	-	150 - 200 (1)		150 - 200
Bulwer's petrel *Bulweria bulwerii*	-	+50	+1 200	+6 000	+3 000	+10 250
Cory's shearwater *Calonectris diomedea*	180 - 200	49 500-89 000	2 000 (1)	+1 500 (1)	13 000	56 000 - 105 700
Manx shearwater *Puffinus puffinus*	-	present	+500 (1)	-	-	+500
Little shearwater *P. assimilis*	-	+150	present	+500 (1)	+3 000 (1)	+3 650
White-faced storm-petrel *Pelagodroma marina*	-	-	-	-	+40 000	+40 000
Madeira's storm-petrel *Oceanodroma castro*	250 - 400	+800	present	+1 000 (1)	+1 000 (1)	3 050 - 3 200
Shag *Phalacrocorax aristotelis*	100 - 150	-	-	-	-	100 - 150
Yellow-legged gull *Larus cachinnans*	10 000 - 20 000	6 415	1 750	2 000	50	20 215 - 30 215
Lesser black-backed gull *L. fuscus*	30 - 60	-	-	-	-	30 - 60
Common tern *Sterna hirundo*	2	4 015	present	+100 (1)	-50	4 200
Roseate tern *S. dougallii*	-	379 - 1 015	present	-	present?	380 - 1 020
Little tern *S. albifrons*	300 - 500 (2)	-	-	-	-	300 - 500
Guillemot *Uria aalge*	15 - 30	-	-	-	-	15 - 30

(1) after Zino & Biscoito (1994); (2) after Leitão et al. (1993); (3) after Monteiro et al. (1996)

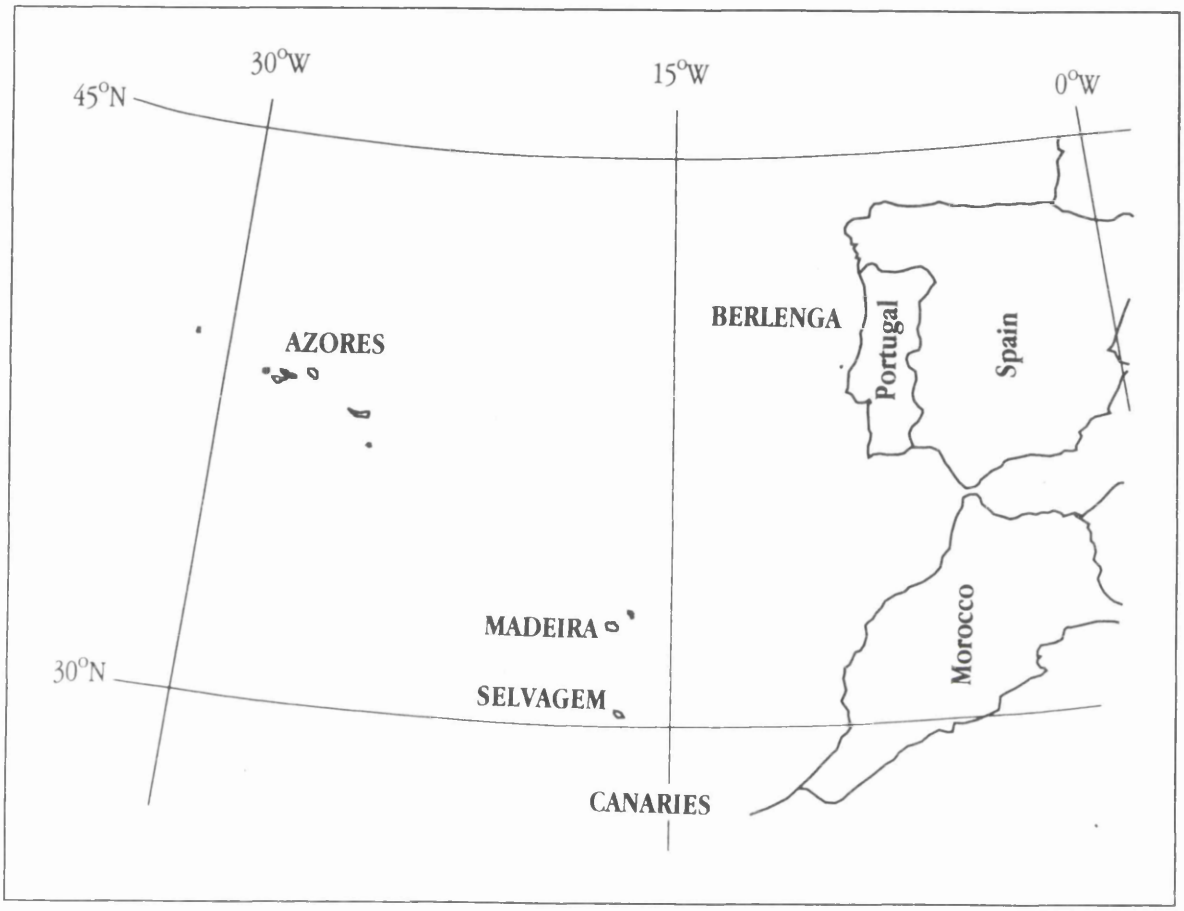

Figure 1. Study area in the Portuguese Atlantic

under the conceptual framework of central place foraging (e.g. Kacelnick 1984, Green and Nunez 1986, Kacelnik & Cuthill 1990). In these long-lived species, undertaking or abandoning a given breeding episode should be decided in relation to the magnitude of the likely risks of increased mortality. Therefore, the decision to return to the colony to incubate the egg or to feed the chick, has to be made in relation to the short-term success of foraging, but long-term effects have also to be considered. The connections between foraging and life-history can therefore be analysed by studying the processes by which adults allocate energy to meet their requirements and those of their chick.

The present thesis was designed as to address some of the questions outlined in previous paragraphs in relation to aspects of the feeding ecology of Cory's shearwater, at several locations in the Portuguese Atlantic. In particular, the thesis is intended to improve the understanding of some processes, by examining the behaviour of individual birds, rather than through indirect evidence as obtained from what the chicks experienced at the nest. The thesis includes descriptive work on biometrics and diet. The latter information required the time-consuming task of establishing and studying an extensive reference collection of fish bones and otoliths from the Azores, Madeira and coastal mainland areas, to enable effective prey identification. This reference collection is currently available at Instituto da Conservação da Natureza, for subsequent studies of diet in piscivorous animals. This research also involved the complete planning and subsequent testing of novel electronic equipment for logging movements of birds entering or leaving their burrows. The development of this technology proved to require adequate computer programming skills, as well as *in situ* efficient electronic problem solving, using the limited available facilities. Finally, this research comprised experimental manipulation of chick condition, as a means to address problems regarding understanding of the regulation of food delivery in Procellariiformes.

The thesis has been produced as a series of chapters, each representing a discrete topic, prepared as a manuscript to be submitted for publication in a scientific journal. For this reason, not all the chapters presented in this thesis are closely related

to each other, and most of them can be read with little cross-reference. The thesis covers the following subjects:

Chapter two analyses morphological variability in Cory's shearwater populations in the Atlantic, and integrates available information from colonies in the Mediterranean. It further presents an effective analytical method to identify males and females from body measurements.

Chapter three presents several relationships used to estimate the size and weight of prey fish from the size of hard structures. It examines bias in dietary studies of piscivorous animals, particularly in seabirds, and discusses the extent to which examining fish vertebrae, in addition to otoliths, can increase accuracy in analysing the diet of marine predators.

Chapter four provides the first quantitative description of the diet of Cory's shearwaters in the Azores archipelago during the breeding season, and puts it into perspective in relation to available evidence on prey of avian and other marine predators in the area.

Chapter five examines the relationship between mercury levels found in prey of several seabird species breeding in the Azores and the levels found in their feathers, as a means of establishing a causal link between accumulation of mercury in tissues and dietary uptake.

Chapter six presents a novel system for real-time automatic logging of arrivals and departures of Cory's shearwaters at their burrows. The system can provide attendance data from several nests simultaneously, and its reliability is quantitatively assessed. Data are presented on attendance of males and females throughout the breeding season, and the potential use of this equipment in behavioural studies of secretive species is discussed.

Chapter seven undertakes a critical examination of the performance of some indirect methods currently used to test hypotheses relating slow chick growth and fat accumulation in Procellariiformes to unpredictable and scarce food supply. These methods are based on periodic weighing of chicks at the nest, and a correct interpretation of the results relies on several assumptions, related to parental behaviour. These assumptions are examined in relation to information provided by

the automatic logging system, and differences in results obtained using different approaches are discussed.

Chapter eight presents evidence on the existence of a flexible foraging strategy in Cory's shearwater. This species was observed to adopt either simple foraging trips (resulting in feeding intervals of up to 3 days), or to present a dual foraging strategy, consisting of alternative short (1-2 days) or long trips (3 to 9 days). This behaviour has not previously been described in any seabird in the Northern hemisphere, though it is found among Southern Ocean Procellariiformes. Some possible reasons for this behaviour and its implications for the understanding of Procellariiform feeding ecology are presented.

Chapter nine describes an experimental protocol to examine whether the rates at which parents provision their chick are under the proximate control of the offspring, or whether they are more likely to be linked to the ability of parents to buffer themselves against increased risks of mortality.

The main findings of these studies are drawn together in a general discussion. Except for the general discussion, all eight main chapters have been or are to be submitted for publication and their format follows that of the corresponding journal. For convenience, references cited in a chapter are listed at the end of that chapter.

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Chapter 2

Variation in measurements of Cory's shearwater between populations and sexing by discriminant analysis

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Granadeiro, J.P. 1993. Variation in measurements of Cory's shearwater between populations and sexing by discriminant analysis. *Ringing & Migration* 14: 103-112

Biometric data were collected at three colonies of the Atlantic race of Cory's Shearwater *Calonectris diomedea borealis*. Significant differences were found between sexes and between study sites. For each colony, a discriminant function was derived in order to achieve external sex identification. Using three measurements, all functions correctly classified more than 95% of the birds of known sex, and the biometrical variables investigated showed no variation with age.

Marked differences in plumage and bill colour, in vocalisation and in size, have led some authors to suggest that Cape Verde *C.d. edwardsii* could be considered as a distinct species. Comparison of morphological data from several colonies of Cory's Shearwater confirmed that the Cape Verde subspecies occupies a very distinct position relative to the Atlantic and the Mediterranean (nominate *C.d. diomedea*) races. Birds from Mediterranean and Atlantic colonies show clinal variation in size, increasing from east to west. This morphological pattern is probably related to biological and physical conditions of the foraging areas of the different colonies.

Like most other Procellariiformes, Cory's shearwater *Calonectris diomedea* shows no sexual dimorphism in plumage characters and although consistent biometrical differences can be found between males and females, it has proved impossible to accurately sex birds using a single morphometric variable.

Discriminant analysis has been widely used to classify seabirds of unknown sex (Dunnet & Anderson 1961, Coulson *et al.* 1983, Scolaro *et al.* 1983, Okill *et al.* 1989, Hamer & Furness 1991). Based on measurements of male and female specimens, this technique produces a discriminant function, which is a linear combination of some metric variables weighted in order to maximise the statistical difference between the sexes (Lachenbruck 1975, Legendre & Legendre 1984, Brennan et *al.* 1991). The optimisation criterion used in the analysis (maximisation of the ratio inter-group variability/intra-group variability) usually enables a much better separation of groups than the methods based on unweighted combination of variables. The variables involved in this kind of analysis must lack temporal and geographical variability (changes with age or season and differences between study sites) and must show strong repeatability of the measurements either by the same or by different workers (Hamer & Furness 1991).

Cory's Shearwaters show clinal variation in size over their geographical range, and therefore a discriminant function derived for one population may not be suitable for application in other colonies. This paper presents biometrical data from adults of the NE Atlantic race of Cory's Shearwater *Calonectris diomedea borealis* at Berlenga (39°24'N, 09°30'W) east Azores (37°45'N, 25°15'W and 36°55'N, 25°10''W) and Salvages (30°09'N, 15°52'W). A separate discriminant function was calculated to allow external sex identification, at each island. Using published data for several other colonies of Cory's Shearwater, the biometrical variation of some Mediterranean and Atlantic populations is also described.

METHODS

Adult birds were caught by hand at their breeding grounds during the night, between 1987 and 1991 (Berlenga), in June 1988 and 1992 (Salvages) and in August

1990 (Azores). At the Azores, birds were captured at Ilhéu de Vila-Franca (San Miguel) and Ilhéu da Vila (St. Maria). These data were pooled, since no significant differences were found between the two sites.

The measurements taken were wing-length (maximum flattened cord), tarsus, culmen-length, distance between anterior edge of nostrils and bill tip (hereafter called nostrils), bill height (measured at the foremost head feathering) and gonys (bill height at the gonys). A stopped wing-rule (readable to 1 mm) and Vernier Callipers (readable to 0.05 mm) were used and the birds were weighed with a Pesola spring balance (readable to 10 g).

Duplicate measurements of 12 birds were taken on Berlenga on two independent occasions, in order to assess measurement consistency, as recommended by Barrett *et al.* (1989). The differences between the two measurements were tested using a paired t-test (Sokal & Rohlf 1981). Another group of 25 birds was measured by the author and by another researcher, in order to evaluate the "resistance" of the discriminant function to inter-observer variability.

Whenever possible, the sex of the birds was identified by their vocalisations, as there are clear differences in the calls (Cramp & Simmons 1977, Ristow & Wink 1980, Bretagnolle & Lequette 1990). The remaining birds were captured during or immediately after copulation. Classification could often be checked later by identifying the sex of both members of pairs.

The influence of age on biometrical variables was tested by comparing the measurements obtained in two consecutive years on the same birds (28 birds), using a Wilcoxon signed-ranks test (Sokal & Rohlf 1981). When the measurements were made more than one year apart, the (theoretical) value for year x+1 (year x = year of the first measurement) was calculated, assuming a linear variation of that structure with time.

After checking the data for normality (using Kolmogorov-Smirnov one-sample tests) and homoscedasticity (using Bartlett's test), One-way Analysis of Variance (ANOVA) was used for comparisons between male and female measurements and between study areas. For significant results of the between-sites

ANOVA, Tukey-Kramer *a posteriori* tests were used, in order to assess which site(s) differed from the other(s). These procedures followed Sokal & Rohlf (1981).

In order to describe the geographical variation of birds from some colonies in the Mediterranean and in the Atlantic, the Average Taxonomic Distance (Sneath & Sokal 1973) was calculated for all pairwise combinations of colonies, using morphometric data (weight, wing-length and culmen-length) published elsewhere. These data were previously standardised (by subtracting the mean and dividing by the standard deviation), to allow comparability of the variables measured in different scales. The dissimilarity values were then arranged on a triangular symmetric matrix, over which a dendrogram was produced, using UPGMA (Unweighed Pair-Group Method using Arithmetic Averages) techniques (Sneath & Sokal 1973). A similar triangular matrix was computed with the distance (in km) between every pair of colonies, using the formula given by Zar (1989). Pearson correlation (Sokal & Rohlf 1981) was then computed between these two sets of data to assess the relation between geographical and taxonomic distances. Statistical significance was defined as a probability of chance occurrence of less than 0.05.

RESULTS

Biometrics of adult birds

Biometrical data of males and females were normally distributed and had equal variance in the three study areas (all Kolmogorov-Smimov and Bartlett's tests gave non significant values). One-way ANOVA was applied to male and female measurements and significant differences were found between the sexes in all study sites (Table 1), males being larger then females in every factor.

The comparison between the colonies of Berlenga, Azores and Salvages also revealed the existence of significant differences in all characters studied (Table 2). Tukey-Kramer *a posteriori* tests (Table 2) indicated that males of Berlenga and Azores were not significantly different and that those of Berlenga were smaller than those from the Salvages. Except for the wing and culmen-length, the males of Azores

were also smaller than those of Salvages. Comparison of female measurements showed a rather similar pattern (Table 2), except for the nostrils and bill-height, where the measurements of the group Azores-Salvages were significantly larger than those obtained at Berlenga.

Measurement repeatability, seasonality and age effects

Independent duplicate measurements of culmen, nostrils, bill-height and gonys were made on 12 birds on Berlenga in 1992. No significant differences were found between the two sets of measurements (Table 3). Furthermore, absolute differences between pairs of measurements of the same individual were consistently small, representing 0.7 to 1.2% of the mean measurements (Table 3), indicating a reasonable measurer consistency for these characters. Weight was not included in the discriminant analysis, since it can change with the nutritional status and date (Fig. 1). Wing-length was excluded due to possible abrasion of the flight-feathers.

Bill characters were tested for possible changes (increase or decrease) with age, using two sets of measurements on the same birds, obtained on consecutive years. No significant variations were detected (none of the Wilcoxon signed-ranks tests were significant), indicating that these variables were adequate for inclusion in the discriminant analysis.

Discriminant analysis

Three discriminant functions were calculated, one for each island. Four variables were initially included in the analysis, but the best discrimination was achieved using culmen length, bill-height and gonys. These variables showed the highest *F*s values in inter-sex comparisons (Table 1). Table 4 shows the equations obtained for each island. Birds with positive discriminant scores (DS) were classified as males, and those with negative scores as females.

All functions were able to classify more than 95% of the cases correctly (Table 4). A global function was calculated, involving the birds of known sex from

the three islands (Table 4). Despite the existence of significant differences in the size of birds from different colonies, the global discriminant function achieved a good separation of the sexes (96.8% correctly classified). In all cases the discriminant scores showed a clear bimodal distribution (Fig. 2).

The function obtained on Berlenga was applied to a separate group of 25 birds independently measured by the author and by another researcher. All discriminant scores calculated with the two sets of measurements gave identical classification of the birds, indicating a good applicability of this function by other workers.

Geographical variation

In order to compare measurements of Cory's Shearwaters from colonies in the Mediterranean and in the Atlantic, data were compiled from several works (Fig. 3). Based on standardised values of the culmen and wing-length a dissimilarity was calculated, over which a dendrogram was produced (Fig. 3), representing morphological similarity patterns of colonies of Cory's Shearwater. The dendrogram clearly defines three groups, corresponding to the bigger and heavier Atlantic race *C.d. borealis* (Berlenga-Azores-Salvages), the isolated Cape Verde subspecies *C.d. edwardsii*, with the smallest birds, and the Mediterranean nominate race *C.d. diomedea* (all others), showing an intermediate size. Within the Mediterranean race, the colony of Paximada (Greece) occupies a rather distinct position (Fig. 3) due to the comparatively small size of the birds. In the Atlantic group, Berlenga and Azores were the most similar, which agrees with previous findings (see Table 2).

Excluding the Cape Verde population, which shows a large morphological separation from all others (Fig. 3), a significant linear correlation was found between the pairwise taxonomic distances and the corresponding geographical distances (r =0.81, $P < 0.001$, with 34 degrees of freedom, Fig. 4), indicating that a significant proportion of the biometrical variation can be explained by the spatial distribution of the colonies.

DISCUSSION

Male and female Cory's Shearwaters from the three studied Atlantic islands show significant differences in all biometrical characters considered. However, there is some overlap between the sexes, preventing external sex identification based on a single measurement.

The discriminant functions obtained in each island correctly classified a high proportion (more than 95%) of the birds of known sex. Although the efficiency calculated using the birds involved in the discriminant analysis tends to overestimate the performance of the method (Lachenbruck 1975), this is a more powerful tool, achieving better results than the techniques based on simple unweighed combinations of variables (*e.g.* Ristow & Wink 1980, Massa & Lo Valvo 1986, Mougin *et al.* 1986). Finally, the large differences between male and female measurements, which resulted in a small overlap of the corresponding discriminant scores, decreased the adverse effects of the morphometric variation between the colonies on the final quality of the discrimination. Due to its efficiency, this method is a good alternative to those based on cloacal examination, which are possible only a short time after laying (*e.g.* Serventy 1956) or laparoscopy (*e.g.* Richner 1989).

Mougin *et al.* (1986) showed that the overlap between male and female scores (calculated as culmen x gonys), increased with increasing sample size. This overlap stabilised after about 300 measurements and the asymptotic misclassification rate obtained was *ca.* 35%. In my study, the classification efficiencies obtained were not significantly different among the three areas, indicating an independent behaviour with sample size and also a comparatively higher performance of the discriminant functions. The biometrical characters involved in the analysis also showed strong consistency and repeatability and lack of variation with age.

Multivariate intercolony comparison clearly identified the three stated subspecies (Cramp & Simmons 1977) and a significant proportion of the morphometric differences is explained by the geographical distribution of the colonies (Fig. 4). However, the Cape Verde population occupies a very distinct position relative to all other colonies. Genetic variability in Cory's Shearwater has been

analysed by Randi *et al.* (1989) but the Cape Verde subspecies *C.d. edwardsii* was not included in their work and so no statements can be made on the genetic isolation of this colony. This population shows striking differences in the colour of bill and plumage, in size, in vocalisation and probably also in their breeding biology traits (Bourne 1955, Bannerman & Bannerman 1968, Cramp & Simmons 1977). These facts led some authors to suggest that this race could be considered as a distinct species (Bannerman & Bannerman 1968, Mougin *et al.* 1991), although Bourne (1986) disagreed with this and presented arguments supporting the preservation of the sub-specific status. More work is needed to evaluate whether the morphological differences between the Cape Verde population and the remaining Atlantic and Mediterranean populations have a consistent genetic basis in order to define clearly its taxonomic status.

Significant biometrical differences between the birds of Berlenga and those of Salvages have already been reported (Granadeiro 1991 a). The birds of Salvages were heavier and bigger and the inclusion of the Azores showed that colonies in these islands have an intermediate position, in average being closer to birds from Berlenga island. However, it is unlikely that significant genetic differences occur within the Atlantic race *borealis*, since Randi *et al.* (1989) have shown that the magnitude of the genetic differences between two Mediterranean colonies and the Azores population was near the mean value among avian subspecies and occasional movements of individuals seems to occur (Granadeiro 1991b).

Biometrical differences between the shearwater colonies can be maintained due to philopatric behaviour of the birds, strong mate and nest site tenacity (*e.g.* Mougin *et al.* 1987, Zammit & Borg 1987) and to the discrete distribution of the colonies. Moreover, Bretagnolle & Lequette (1990) suggested the existence of behavioural isolation mechanisms, related to the development of local call dialects. In fact, movements within and between the Atlantic and the Mediterranean colonies are rather uncommon (Lo Valvo & Massa 1988, Granadeiro 1991b), and these tend to involve mainly non-breeding birds. Physical and biological conditions prevailing in the foraging areas of the different colonies may be a major factor explaining the biometrical cline observed from the East Mediterranean to the Atlantic (Iapichino *et*

al. 1983) and the availability and quantity of food resources may act as a fundamental environment variable, determining this particular morphological pattern.

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Table 1. Weight and measurements of male and female Cory's shearwaters from Berlenga, Azores and Salvages. Significant F_S values (One-way ANOVA) are indicated (*** - P<0.001). Weight in g, all other measurements in mm.

Berlenga

	Males			Females			
	Mean	s	n	Mean	s	n	F_S
Wing	369.8	7.56	80	359.6	7.48	80	73.0***
Weight	868.6	76.72	81	742.2	53.49	82	149.3***
Tarsus	58.93	1.755	30	56.53	1.322	33	37.8***
Culmen	56.27	1.847	82	52.95	1.624	81	148.6***
Nostrils	43.86	1.606	82	41.28	1.275	80	128.3***
Height	21.64	0.851	82	19.39	0.581	81	388.6***
Gonys	16.39	0.638	82	14.79	0.484	80	323.3***

Azores

	Males			Females			
	Mean	s	n	Mean	s	n	F_S
Wing	372.5	6.68	22	363.2	6.91	20	19.6***
Weight	880.0	66.05	17	747.5	52.07	12	33.5***
Culmen	56.82	1.906	22	53.15	1.337	20	51.1***
Nostrils	44.6	1.857	22	42.20	1.413	20	21.9***
Height	21.6	0.588	22	19.81	0.588	20	97.9***
Gonys	16.65	0.394	22	15.00	0.446	20	162.3***

Salvages

	Males			Females			
	Mean	s	n	Mean	s	n	F_S
Wing	375.8	6.97	38	367.0	7.57	46	30.5***
Weight	948.6	85.43	38	836.1	69.23	46	43.1***
Tarsus	60.85	1.606	34	58.16	1.786	46	45.7***
Culmen	57.42	2.332	38	53.73	1.642	46	71.9***
Nostrils	45.76	2.142	38	42.38	1.968	46	56.9***
Height	22.49	0.763	38	19.93	0.431	46	374.9***
Gonys	17.31	0.589	38	15.52	0.499	46	227.6***

Table 2. Intercolony measurement comparisons for each sex, using One-way ANOVA (see Table 1). Significant F_S values are indicated (* - P<0.01; *** - P<0.001). Colonies linked by dark bars are not significantly different (Tukey-Kramer tests). Weight in g, all other measurements in mm.

Males

	Berlenga	Azores	Salvages	F_S
Wing				9.2***
Weight				13.2***
Culmen				4.4*
Nostrils				14.5***
Height				16.4***
Gonys				30.6***

Females

	Berlenga	Azores	Salvages	F_S
Wing				14.7***
Weight				38.5***
Culmen				3.6*
Nostrils				8.3***
Height				16.4***
Gonys				32.7***

Table 3. Comparison between first and duplicate measurements made on 12 birds of Berlenga, using Paired t-tests (ns - not significant). All measurements in mm.

	1st Measurement		2nd Measurement		Absolute Difference		% of 1st Measurement	Paired t-test
	Mean	sd	Mean	sd	Mean	sd		
Culmen	54.15	2.918	54.44	2.728	0.37	0.294	0.68	1.16^{ns}
Nostrils	42.65	2.003	42.85	1.929	0.50	0.371	1.17	0.97^{ns}
Height	20.79	1.247	20.68	1.196	0.16	0.217	0.77	-1.65^{ns}
Gonys	16.00	0.925	16.03	0.988	0.16	0.082	1.00	0.70^{ns}

Table 4. Equations used to calculate the discriminant scores (DS) of birds of Berlenga, Azores and Salvages, and for all birds from the three areas (Total). Sample sizes (n) and proportion of correctly classified cases are indicated. All measurements in mm.

Colony	Discriminant function	Correctly Class. cases	n
Berlenga	DS=0.201xCulmen+0.728xHeight+0.858xGonys+39.347	96.9%	161
Azores	DS=0.137xCulmen+0.514xHeight+1.682xGonys+45.039	97.6%	42
Salvages	DS=0.087xCulmen+1.206xHeight+0.598xGonys+40.063	98.8%	84
Total	DS=0.159xCulmen+0.896xHeight+0.458xGonys+34.568	96.8%	287

Figure 1. Variation in male and female weight (mean±standard error) on Berlenga island in 1991. Sample sizes are indicated.

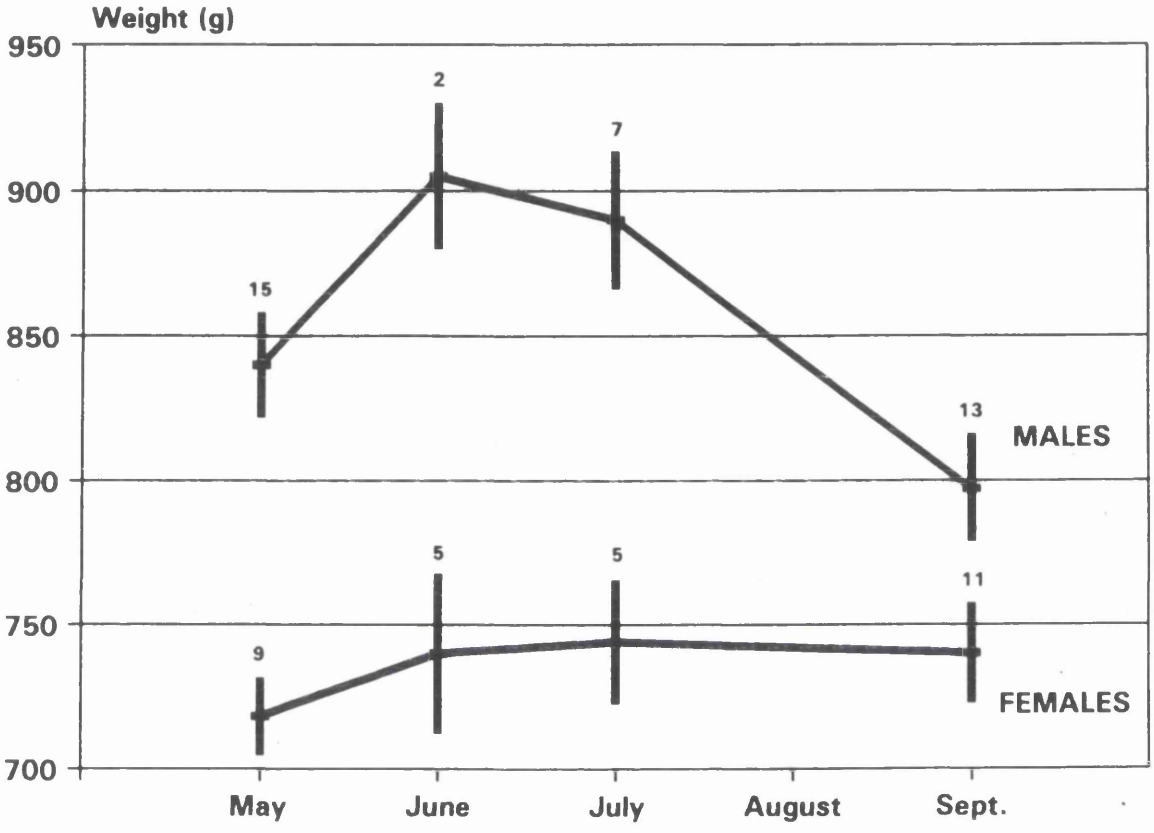


Figure 2. Distribution of male and female discriminant scores obtained in the three islands and with an overall discriminant function. For each sex, sample sizes are indicated.

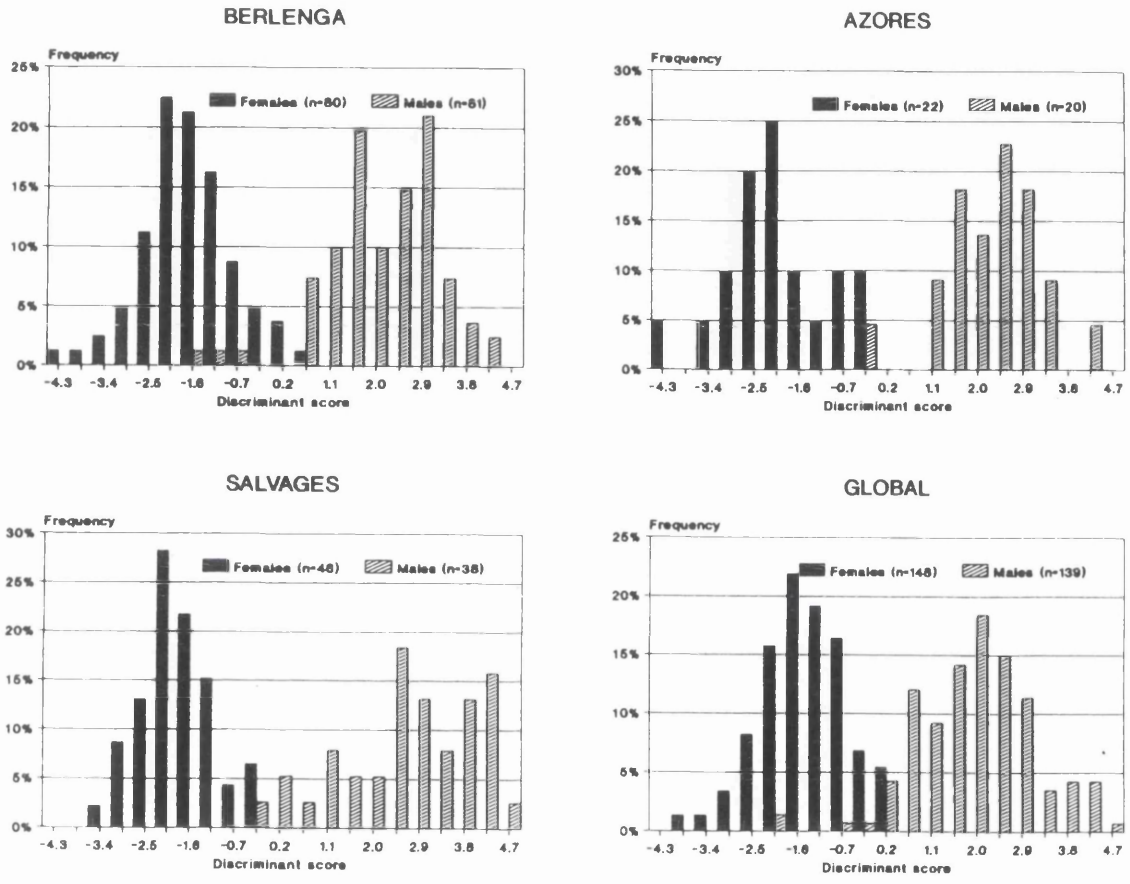


Figure 3. Morphological "similarity" pattern of several colonies from the Mediterranean (*C.d.diomedea*), the Atlantic (*C.d.borealis*) and Cape Verde (*C.d.edwardsii*) - (see Methods). Biometrical data from Cramp & Simmons (1977), Ristow & Wink (1980), Iapichino *et al.* (1983), Massa & Lo Valvo (1986) and this study.

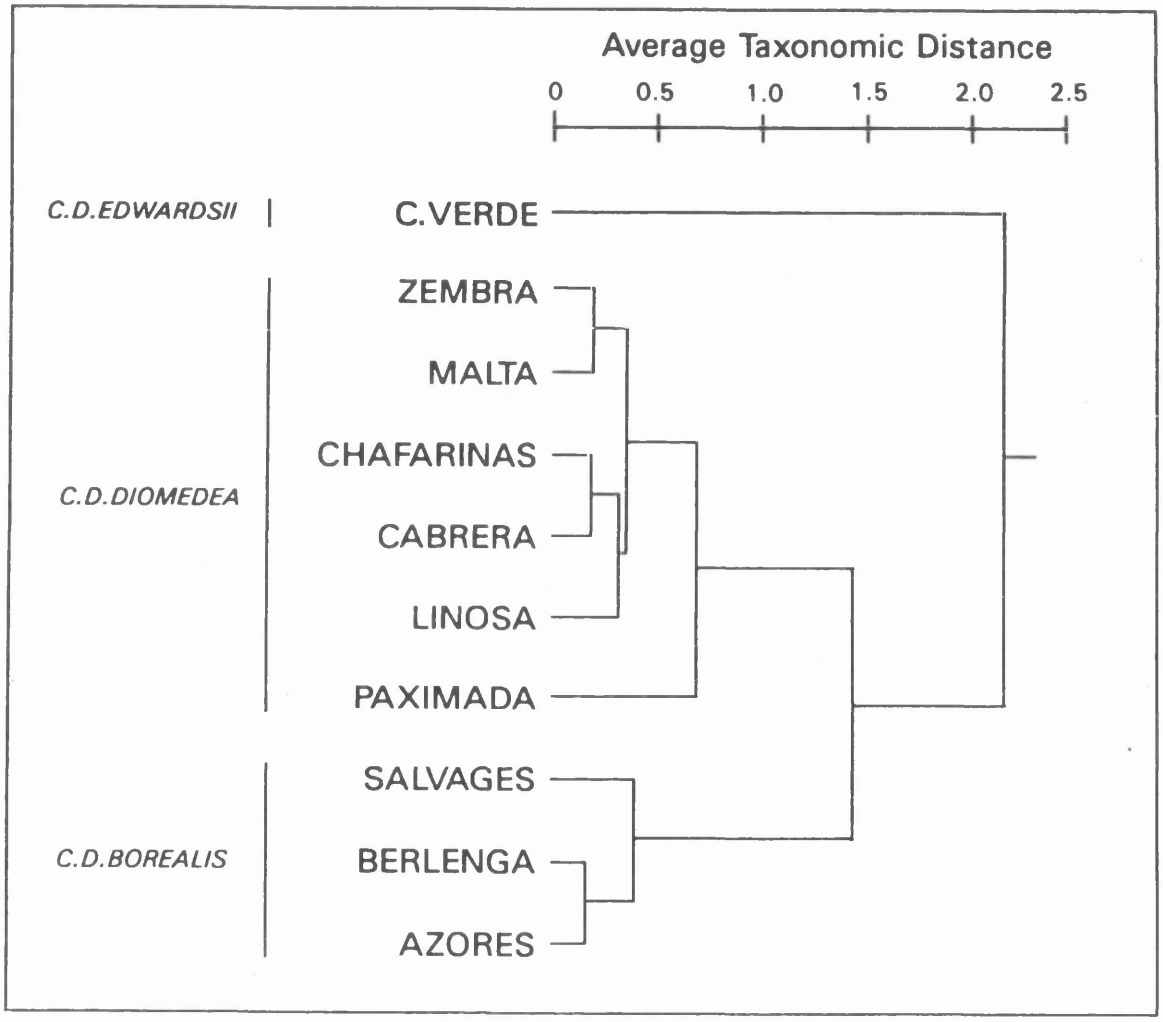
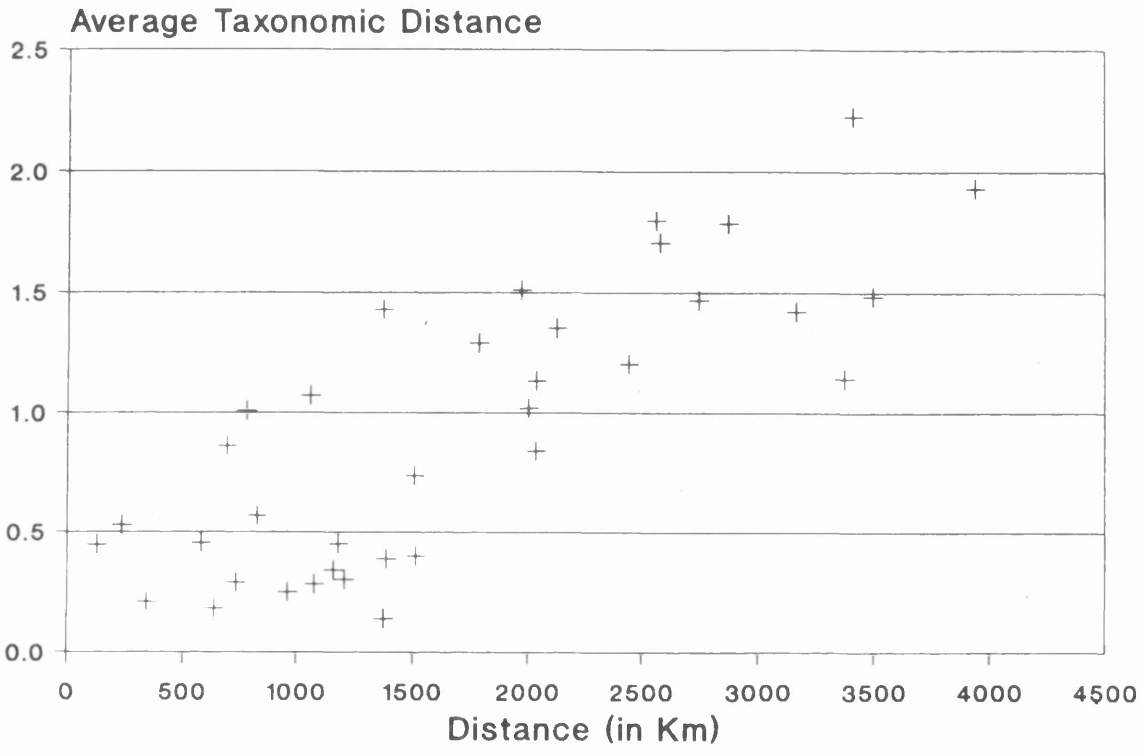


Figure 4. Relationship between geographical distance (in Km) among all pairs of islands and the corresponding Average Taxonomic Distances (see Methods).



Chapter 3

Use of otoliths and vertebrae to identify and estimate size of fish

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Granadeiro, J.P. & Silva, M.A. Use of otoliths and vertebrae to identify and estimate size of fish

Relationship between size of hard structures (otoliths and vertebrae) and body dimension and weight were calculated for eleven fish species of the north-east Atlantic. These equations can be used to reconstruct the original dimensions of prey fish from the size of hard structures found in food samples of marine piscivores.

For each fish species we selected those hard structures which possessed unique features enabling diagnosis of specimens to the level of genus or species. Linear and curvilinear relationships with structure size provided the best fit to estimate fish length, and power functions yielded the best predictors for fish weight. Comparison between equations obtained in this study and similar functions calculated for the same species at different locations, revealed consistent geographical differences in the structure size/body dimension relationships. This calls for caution when using equations derived by other author on geographically distinct populations, especially if precise quantitative data are required (e.g. for bioenergetic studies).

INTRODUCTION

Dietary studies of piscivores are often limited by the difficulty to obtain food samples in such condition that identification of prey species is possible. Most diet work rely on the identification of hard parts (e.g. otoliths, scales and bones) found in food samples (Recchia & Read, 1989; Prime & Hammond, 1990; Pierce & Boyle, 1991).

Several methods have been proposed for the analysis of the diet of predatory fishes, seabirds and marine mammals and these have been extensively reviewed by Hyslop (1980), Duffy & Jackson (1986) and Pierce & Boyle (1991), respectively. These authors provided a comprehensive description of available methods along with their potential biases and limitations and presented guidelines to overcome some of the analytical problems. They were unanimous in recognising that otoliths are the most widely used structures for fish prey identification in dietary studies. The size and shape of otoliths often enable fish identification to the level of genus or species and this has encouraged the production of keys and guides for a variety of fish species (e.g. Nolf, 1985; Härkönen, 1986).

Otoliths can also be used to reconstruct the original dimensions of the prey. Fish size and/or weight can be regressed on an appropriate otolith measurement (length, width, thickness or weight) and these relationships can be used to estimate the original dimensions of individuals found in food samples (e.g. Nolf, 1985; Pierce & Boyle, 1991 and references therein; Brown & Pierce, 1997; Tollit et al., 1997). In addition to otoliths, other hard structures have also been used as a means of providing further possibilities of prey identification and to account for situations in which, for some reason, otoliths can not be used to reconstruct fish size (Pierce & Boyle, 1991). Among these structures, fish vertebrae are clearly the most widely used (Casteel, 1976; Watson, 1978; Pierce & Boyle, 1991; Watt et al., 1997). In fact, vertebrae possess characteristic diagnostic features that potentially enable prey identification, frequently to the level of species. They have the advantage of being formed of calcium phosphate, and might thus be expected to be less digestible than otoliths (Pierce et al., 1993), which are made of calcium carbonate. The use of vertebrae in dietary analysis in addition to otoliths can greatly increase the possibility of including

otherwise undetectable fish species (Pierce et al., 1993; J.P.G. & M.A.S., personal observations) and of producing more accurate estimates of the minimum number of prey consumed (Feltham & Marquiss, 1989; Feltham, 1990; J.P.G. & M.A.S., personal observations). They also provide the possibility to cross-validate fish size estimates based on otolith measurements.

For many fish species there are still no published relationships between otolith size and body dimensions (but see Härkönen, 1986; Feltham & Marquiss, 1989; Recchia & Read, 1989; Gamboa, 1991; Plötz, Ekau & Reijnders, 1991; Hammond et al., 1994 a,b; Brown & Pierce, 1997; Tollit et al., 1997) and the same stands for relationships involving vertebrae (but see Casteel, 1976; Wise, 1980; Feltham & Marquiss, 1989; Watt et al., 1997). In this paper, we present relationships between otolith size and fish dimensions for some common species occurring in the North-eastern Atlantic. We also describe the use of diagnosing vertebrae in dietary studies to aid prey identification and also to back-calculate the original dimensions of some fish species.

METHODS

We selected eleven fish species which could be easily identified from diagnosing features of otolith (blue whiting *Micromesistius poutassou* (Risso, 1826), n=240, pouting *Trisopterus luscus* (L., 1758), n=50, European hake *Merluccius merluccius* (L., 1758), n=54), vertebrae (sardine *Sardina pilchardus* (Walbaum 1792), n=86, boar fish *Capros aper* (L., 1758), n=30, snipe fish *Macroramphosus scolopax* (L., 1758)/*M. gracilis* (Lowe,1839), n=40, chub mackerel *Scomber japonicus* (Houttuyn, 1782), n=32, Atlantic mackerel *S. scombrus* (L., 1758), n=28) or both (horse mackerel *Trachurus trachurus* (L., 1758), n=39, Mediterranean horse mackerel *T. mediterraneus* (Steindachner, 1869), n=11, blue jack mackerel *T. picturatus* (Bowdich, 1825), n=10). This selection was based on preliminary observations on their importance in the diet of pelagic seabirds and marine mammals off the Portuguese coast (unpublished data) and also on their known abundance in this area (e.g. Anon., 1997). There is still some debate about the taxonomic

separation of *Macroramphosus scolopax* and *M. gracilis* (e.g. Ehrich, 1975; Brêthes, 1979) so in this study this group will be referred to as *Macroramphosus* species.

Most fish used in this study were obtained in fishing operations during acoustic surveys off the Portuguese continental shelf, carried out by the R/V Noruega of Instituto de Investigação das Pescas e do Mar. We supplemented sample collection using specimens available at the local market, also caught off the Portuguese coast. Most fish were deep frozen after collection until analysis and some specimens (<15%) were analysed fresh. We measured total fish length (to the nearest millimetre) on all species except boar fish and snipe fish, for which standard length was used, because they frequently had their caudal fins damaged. The specimens were then weighed to the nearest 0.1 g (boar fish and snipe fish) or 0.01 g (all other species), and cooked in a microwave oven. The microwave oven was preferred to boiling because it does not cause distortion of the bone shape (Pierce et al., 1993). The otoliths were extracted and the flesh was carefully removed with forceps and a soft brush. Otoliths (maximum length) and vertebrae (centrum length or centrum width, in the case of the sardine) were measured under a binocular microscope fitted with an eye-piece graticule, to the nearest 0.02 mm, and preserved dry.

For each species, we selected structures which were most likely to be found and identified in food remains of fish-eating birds and marine mammals (unpublished data). Otoliths of sardine, boar fish, snipe fish and Scombrid species are very small and fragile and therefore we did not calculate relationships for these species using this structure. Furthermore, we just present relationships with vertebrae that could be individually identified among all others, even when the fish skeleton was entirely disarticulated. Vertebrae identification was based on several diagnosing features such as waisting and sculpturing of the centrum, development and orientation of dorsal and/or ventral zigapophyses, size and shape of neural and haemal spines and position and size of foramina (see Figure 1).

We tested both linear and non-linear relationships of fish size and otolith/vertebra dimensions (length and width). The same procedure was applied to fish-size/fish-weight relationships, which were computed for all species studied. In each case we selected those which explained the highest proportion of the variance (highest coefficient of determination, r^2). Statistical procedures followed Zar (1996).

RESULTS

Relationships with otoliths

There was no significant difference in fish size/fish weight relationship obtained for deep frozen and fresh specimens of pouting [Analysis of Covariance (ANCOVA): for slope $F_{1,46}$=0.01, *ns*; for elevation $F_{1,47}$=0.03, *ns*). Therefore we assumed that preservation time did not affect these relationships on the other species, which were kept frozen for similar periods.

Table 1 presents the relationships between otolith length and total length for blue whiting, pouting, European hake, and *Trachurus* species. Distinction between the three *Trachurus* species on the basis of otolith shape is often difficult and therefore, we also calculated a relationship for pooled data from these species (Table 1). This regression also explained a large proportion of the variance (r^2= 0.92, n=60, P<0.001, see Table 1) despite the existence of significant differences in slope of the regression lines obtained for each species (ANCOVA: for slope, $F_{2,54}$=7.11, P<0.01).

Relationships with vertebrae

Figure 1 presents the vertebrae used in those computations, and their relative position in the vertebral column of the fish. We calculated relationships between vertebrae size and fish dimensions for sardine, boar fish, snipe fish, *Trachurus* species and Scombrids (Table 2). Vertebra length provided the best predictor of fish size for all species except sardine, for which we selected vertebra width. All regressions were highly significant (Table 2).

There were significant interspecific differences in the elevation (but not slope) of the regression lines involving vertebrae within genus *Trachurus* (ANCOVA: for elevation, $F_{2,49}$=4.30, P<0.05; for slope, $F_{2,47}$=1.57, *ns*). The vertebra used in this study did not generally allow diagnosis of the specimens to the level of species. We also present a relationship computed on pooled data from these three species which can be used in areas where they all occur. This relationship was also

highly significant (Table 2). No interspecific differences were found in genus *Scomber* (ANCOVA for second vertebra with closed haemal arch: for elevation, $F_{1,50} = 2.15$, *ns*; for slope $F_{1,49} = 0.07$, *ns*; ANCOVA for first caudal vertebra: for elevation, $F_{1,50} = 1.46$, *ns*; for slope, $F_{1,49} = 0.66$, *ns*). Therefore, we also present a regression line for data pooled from both species (Table 2).

Table 3 presents the relationships between fish (standard or total) length and fish weight for the species studied. All regressions were highly significant.

DISCUSSION

All fitted functions relating otolith length with fish size explained a very large proportion of the variance in the data, which confirms the applicability of this approach for estimating the size of prey fish. Although linear functions are usually employed to describe these relationships (e.g. Casteel, 1976; Härkönen, 1986; Hammond et al. 1994 a,b; Brown & Pierce, 1997; Tollit et al., 1997), in this study curvilinear functions provided the best fit for blue whiting and European hake. Härkönen (1986) also computed linear functions for these two species. However, within the common range of otoliths size, the equations presented in this study for both species yielded length estimates that differed by 1%-14% (in relation to the higher estimate) from those of Härkönen (1986). In the absence of the raw data no statistical analysis was possible, but the equations derived by Härkönen (1986) showed a consistent (positive) difference in elevation, but apparently not in slope. These allometric discrepancies seem to confirm the lack of geographical uniformity in the relationships between otolith size and fish size in populations of widely distributed fish species (Härkönen, 1986). This calls for caution in order to ensure the use of appropriate local relationships when estimating fish size from otolith measurements.

Most published studies on the diet of piscivorous animals have used otoliths for prey identification (reviews in Hyslop, 1980; Duffy & Jackson, 1986; Pierce & Boyle, 1991). Some identification keys and otolith size/fish size relationships are currently available (Härkönen, 1986; Gamboa, 1991; Brown & Pierce, 1997; Tollit et al., 1997), but they are usually restricted to some species or study areas. Moreover

they generally do not take into account ontogenetic changes occurring during fish growth (Nolf, 1985; Pierce et al., 1991a) and these factors limit their general applicability. Despite being the most dense structures in the body of teleostean fish (Treacy & Crawford, 1981), otoliths are not very resistant to acidic digestion (Pierce & Boyle, 1991; Pierce et al., 1993). They can suffer varying degrees of digestion before being available for analysis, sometimes leading to small otoliths being completely dissolved and the corresponding species undetected in the samples. Partial digestion will bias estimates of prey size (da Silva & Neilson, 1985; Jobling & Breiby, 1986; Pierce & Boyle, 1991; Pierce et al., 1993) and can even prevent identification. Correction factors have been derived using feeding experiments with captive animals (mainly pinnipeds), to minimise errors arising due to otolith digestion (e.g. Prime & Hammond, 1990; Hammond et al., 1994 a,b; Tollit et al., 1997). These procedures can significantly increase the accuracy of fish size estimates, but to ensure maximum efficiency they require complex calibration work in order to control for differences in predator and prey species, size of preys and degree of digestion of hard remains (e.g. Tollit et al., 1997 and references therein), which is unfeasible for many fish predators. In addition to acid digestion, otoliths can became physically damaged during the process of ingestion or during sample collection and processing, in which case reconstructing fish size and even identifying the prey can be rendered impossible.

These facts have led to an increasing number of studies using alternative hard remains as a means to provide a more accurate description and quantification of the diets of piscivores. Vertebrae of studied species possess diagnosing characters allowing identification to the level of species or genus, emphasising their potential use for identification in dietary studies of piscivores animals. The vertebrae used in this study showed no major variation in form and shape with fish size, as found by Hansel et al. (1998) and this made identification reliable and relatively simple. As very few keys for identification of fish bones are available (but see Newsome, 1977; Watson, 1978; Borodulina, 1984; Hansel et al., 1988; Watt et al., 1997), the construction of a reference collection is strongly recommended to assess inter- and intra-specific variability in bone shape. After some familiarisation, it was even

possible to identify fragments of vertebrae, as long as some details of their structure were not destroyed.

Vertebrae can be used to estimate the size of prey, enabling cross-validation of size estimates obtained from otoliths. Bones are potentially less affected by acidic digestion than otoliths, because they are composed of calcium phosphate (Pierce et al., 1993) and often present multiple identification elements. *In vitro* (Pierce et al., 1993) and *in vivo* (Pierce et al., 1993; Carss & Elston, 1996) experiments provided some evidence of the higher resistance of bones, but more work is needed to validate the use of vertebrae as a means to estimated the size of prey fish and to derive adequate correction factors.

All relationships between fish size and vertebrae dimensions explained a large proportion of the variance in the data, even when information from related species were pooled (*Trachurus* species and Scombrids) and so this structure provides a reliable tool for reconstructing the original dimensions of fish prey. If positive identification of the vertebrae used to derive the regressions is not possible, the closest vertebrae should be used, since there seems to be little variation in the centrum size between adjacent vertebrae (Watt et al., 1997). Relationships with vertebrae are particularly adequate to estimate the size of species with small otoliths, such as sardine, Scombrids, boar fish and snipe fish, which constitutes preferred preys for several marine mammals and seabird species off the Portuguese coast (unpublished data) and probably in many subtropical areas of the North-eastern Atlantic.

To our knowledge there are no published relationships between vertebra size and fish length for the species presented in this study, so we can not assess whether a geographic variation similar to that recorded in otoliths exists. However, the relationships between fish length and vertebra length are probably much more constant then those involving otoliths (at least if different populations fail to exhibit geographical variation in the number of vertebrae), as they represent a "structural" component of fish total length (see Ford, 1937).

Fish weight can be estimated directly by regressing it on a given structure dimension (length or width), or indirectly deriving it by using a relationship between the structure size and fish size and then a fish size/fish weight equation (Casteel,

1976). The use of two regressions instead of a direct one may introduce additional errors (Casteel, 1976; Pierce & Boyle, 1991). However, there is generally considerable seasonal and geographical variation in fish size/fish weight relationships (e.g. Coull et al., 1989; Pierce et al., 1991b). Therefore, the use of two functions is recommended, when one intends to estimate fish weight based on regressions derived for other areas.

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Table 1. *Relationships between otolith length (OL) and fish total length (TL) (both in mm). Coefficient of determination (r^2) and sample sizes (n) are indicated. The regression equations presented are those with the highest r^2. All regressions significant at P<0.0001.*

Common name	Regression	r^2	*n*	Range of length (mm)
Blue whiting	$TL = 14.49 * OL^{1.13}$	0.95	240	TL= 120-249
Pouting	TL= 33.73 * OL - 94.54	0.94	50	TL= 102-340
European hake	$TL = 19.06 * OL^{1.05}$	0.99	54	TL= 109-512
Horse mackerel	TL= 34.01 * OL - 28.99	0.95	39	TL=114-353
Blue jack mackerel	TL= 40.09 * OL - 37.15	0.97	10	TL= 120-353
Mediterranean horse mackerel	TL= 43.05 * OL - 71.28	0.98	11	TL=120-335
Trachurus species combined	TL= 35.49 * OL - 30.99	0.92	60	TL= 114-353

Table 2. *Relationships between vertebra dimensions and fish length (both in mm). All equations used vertebra length as the independent variable, except for sardine where vertebra width was chosen. Coefficient of determination (r^2) and sample sizes (n) are indicated. The regression equations presented are those with the highest r^2. TL= total length, SL= standard length, VW= vertebra width, VL= vertebra length. All regressions significant at P<0.0001.*

Common name	Vertebra	Regression	r^2	*n*	Range of length (mm)
Sardine	atlas	TL= 50.06 * VW + 23.31	0.93	86	TL= 79-219
Boar fish	fourth	SL= 34.36 * VL + 10.48	0.91	30	SL= 65-94
	fifth	SL= 32.64 * VL + 9.37	0.90	30	SL= 65-94
	first caudal	SL= 33.06 * VL + 11.97	0.92	30	SL= 65-94
Snipe fish	fifth	SL= 31.41 * VL + 15.92	0.97	40	SL= 48-146
	first caudal	SL= 55.16 * VL - 2.37	0.97	40	SL= 48-146
Horse mackerel	first caudal	TL= 36.58 * VL + 6.17	0.93	32	TL=114-268
Blue jack mackerel	first caudal	TL= 32.23 * VL + 19.37	0.96	10	TL= 129-270
Mediterranean horse mackerel	first caudal	TL= 33.60 * VL + 13.70	0.99	11	TL= 120-335
Trachurus species combined	first caudal	TL= 33.21 * VL + 18.91	0.97	53	TL= 114-335
Atlantic mackerel	2nd with closed haemal arch	TL= 34.79 * VL + 36.51	0.97	21	TL= 178-365
	first caudal	TL= 34.49 * VL + 38.53	0.97	21	TL= 178-365
Chub mackerel	2nd with closed haemal arch	TL= 34.34 * VL + 42.00	0.97	32	TL= 201-385
	first caudal	TL= 33.22 * VL + 47.79	0.97	32	TL= 201-385
Scomber species combined	2nd with closed haemal arch	TL= 34.24 * VL + 41.55	0.97	53	TL= 178-385
	first caudal	TL= 33.70 * VL + 44.47	0.98	53	TL= 178-385

Table 3. *Relationships between fish length (in mm) and fish fresh weight (in g). All equations used fish total length (TL) as the independent variable, except for boar fish and snipe fish where standard length (SL) was used instead. Coefficient of determination (r^2) and sample sizes (n) are indicated. The regression equations presented are those with the highest r^2. All regressions significant at $P<0.0001$.*

Common name	Regression	r^2	*n*	Range of weight
Sardine	$W= 6.92*10^{(-6)} * TL^{3.03}$	0.92	81	W= 17.0-89.3 g
Boar fish	$W= 7.64*10^{(-5)} * SL^{2.83}$	0.95	30	W= 10.3-27.8 g
Snipe fish	$W= 2.98*10^{(-5)} * SL^{2.67}$	0.98	40	W= 0.9-17.9 g
Blue whiting	$W= 3.40*10^{(-6)} * TL^{3.09}$	0.99	240	W= 9.6-80.6 g
Pouting	$W= 4.33*10^{(-6)} * TL^{3.19}$	0.99	50	W= 10.5-532.4 g
European hake	$W= 2.30*10^{(-6)} * TL^{3.18}$	0.99	54	W= 7.3-921.4 g
Horse mackerel	$W= 1.77*10^{(-5)} * TL^{2.84}$	0.99	39	W= 11.5-333.2 g
Blue jack mackerel	$W= 1.53*10^{(-5)} * TL^{2.87}$	0.99	10	W= 17.7-146.5 g
Mediterranean horse mackerel	$W= 8.18*10^{(-7)} * TL^{3.44}$	0.99	11	W= 14.7-431.7 g
Trachurus species combined	$W= 6.73*10^{(-6)} * TL^{3.03}$	0.98	60	W= 11.5-431.7 g
Atlantic mackerel	$W= 1.12*10^{(-7)} * TL^{3.75}$	0.97	28	W= 33.4-421.1 g
Chub mackerel	$W= 4.73*10^{(-8)} * TL^{3.90}$	0.93	32	W= 44.1-520.4 g
Scomber species combined	$W= 8.00*10^{(-8)} * TL^{3.81}$	0.95	60	W= 33.4-520.4 g

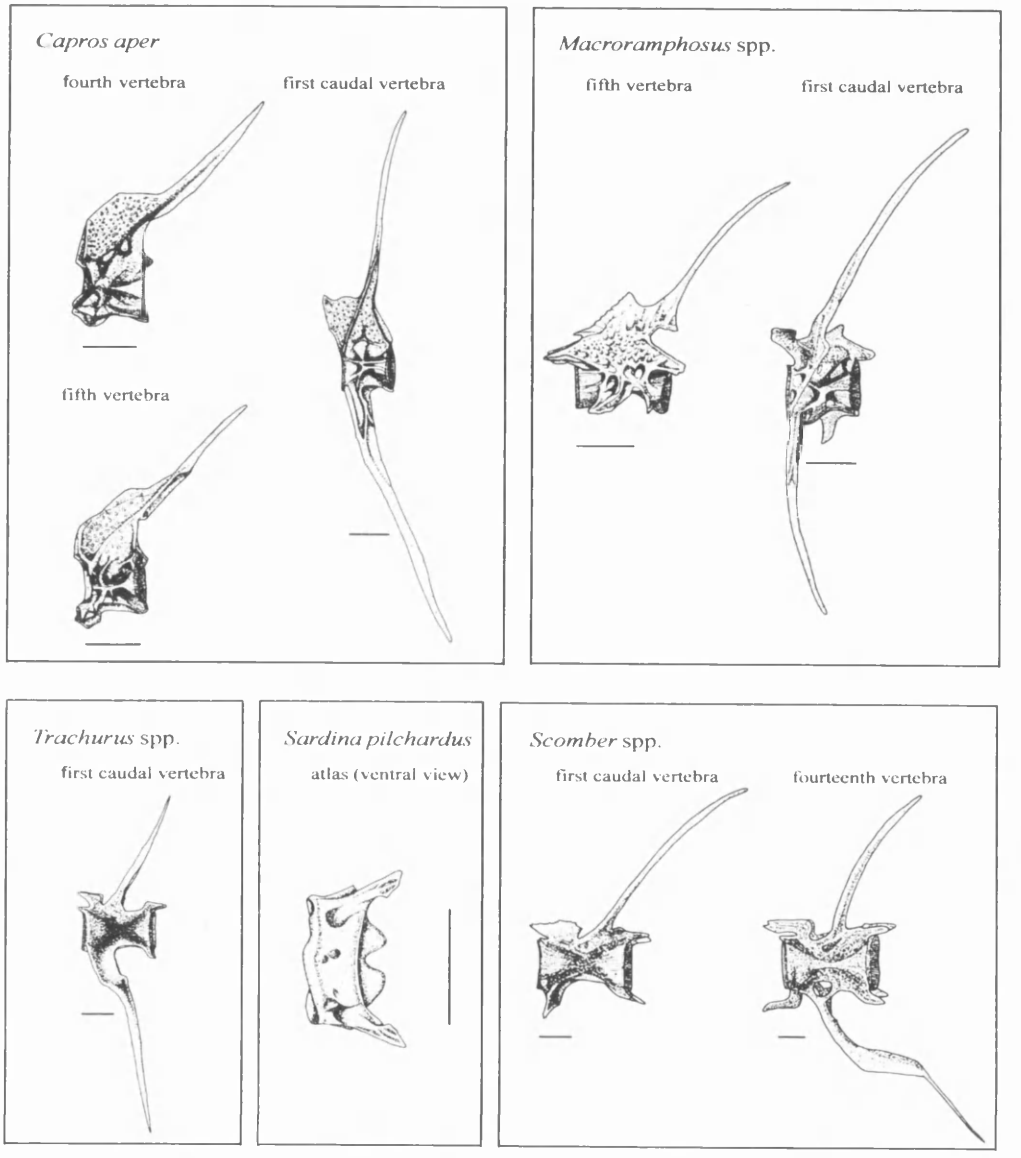

Figure 1. Ventral view of sardine atlas and lateral views of vertebrae of boar fish, snipe fish, *Trachurus* species and *Scomber* species. Position of each vertebra in the vertebral column is indicated. Scale bars: 2 mm.

Chapter 4

The diet and feeding ecology of Cory's shearwater *Calonectris diomedea* in the Azores, north-east Atlantic

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ABSTRACT

Cory's shearwater *Calonectris diomedea* is the most abundant pelagic seabird in the Azores archipelago. We examined their diet in March and August. Fish were present in more than 90% of the samples analysed, but included only five species. Two small pelagic species, boarfish *Capros aper* and trumpet fish *Macrorhamphosus* sp. were the most common prey, accounting for more than 85% of the food items consumed in March and August. Due to their small size (<120 mm) these two species only represented about 40% of the diet by weight. Conversely, sauri (*Scomberesox saurus* and *Nanychthys simulans*) represented an important proportion of the diet by weight (25%), despite being consumed in smaller numbers (<5%). Horse mackerel *Trachurus picturatus* and chub mackerel *Scomber japonicus* were consumed in low number and together accounted for 10% of the diet by weight. Twelve cephalopod species occurred in the diet, most having a mesopelagic distribution. It is suggested that these prey are made available to shearwaters when they are driven to the surface by underwater predators. Surprisingly, no deep water fish were detected in Cory's shearwater diet, despite being known to be available to other diurnal surface feeding seabirds in this area. The diet of shearwaters in the Azores is discussed in relation to available information on the prey consumed by other coexisting marine predators. We suggest that Cory's shearwater provide useful and novel information on abundance and distribution of small pelagic fish in this region.

INTRODUCTION

Several studies have demonstrated that seabirds can be used to sample the marine environment (e.g. Ashmole 1971, Furness & Greenwood 1993, Cherel & Weimerskirch 1995, Croxall & Prince 1996, Furness & Camphuysen 1997) and special attention has been devoted to examining the response of seabirds to changing food availability (Hamer et al. 1991, Uttley et al. 1994, Ainley et al. 1995, Phillips et al. 1996). There have been attempts to establish relationships linking avian response to food availability at sea (Montevecchi 1993, Uttley et al. 1994, Phillips et al. 1996). However, modelling such causal relationships requires detailed information on both the biology of seabirds and that of their prey, which is still not available in some regions. The lack of adequate biological data is particularly obvious in areas where there are no fishery interests in exploring local stocks, such as many sub-tropical oceanic waters exhibiting low biological productivity (Montevecchi 1993). This is the case in the pelagic waters surrounding the Azores archipelago (36-39° N, 25-31°W), in the north-east Atlantic, for which there is still a paucity of both oceanographic information and data describing food webs (see Santos et al. 1995 for a review). Recent studies have described the diet of some seabirds in the archipelago (Granadeiro et al. 1995, Monteiro et al. 1996a, Ramos et al. in press a, b). However, most of the seabird species so far examined feed relatively close to breeding colonies and exhibit predominantly coastal feeding behaviour, hence information on seabird prey in oceanic waters is still scarce.

Cory's shearwater *Calonectris diomedea* is a pelagic seabird, breeding in the sub-tropical north-east Atlantic (Cramp & Simmons 1977). The Azores archipelago holds over 70% of the breeding numbers of the Atlantic subspecies *C. diomedea borealis*, currently estimated as 100 000 pairs (Hagemeijer & Blair 1997). Despite being the most abundant seabird in this region, to date there is no quantitative information on its diet at the breeding grounds. Published results mainly report opportunistic observations of feeding behaviour of birds (e.g. Martin 1986), or make a general description of main prey items. Furness (1994) presented a quantitative assessment of squid consumption in the North east Atlantic, presenting data on the

importance of squid in the diet of Cory's shearwater. However, no reference was made to which species of squid are consumed, and these remain totally unknown (review in Croxall & Prince 1996).

Cory's shearwaters can forage over extensive areas (e.g. Mougin & Jouanin 1997) and their abundance suggests that they are important consumers of fish and squid in the pelagic ecosystem (eg Prince & Morgan 1987, Warham 1996). They are generalist surface feeders, and so their diets are likely to reflect short-term variability in food availability. They therefore represent suitable sampling units for the pelagic organisms which constitute their diet. Hence, the study of their diet will add considerable insight into their role in marine food webs, while providing information on the ecological processes which control energy transfer to top predators. In this study we examine the relative importance of cephalopod and fish prey in the diet of Cory's shearwater in the Azores during the breeding season and we estimate the mass of fish consumed annually by this species in this region. We interpret this information in light of current knowledge of the birds' behaviour, that of their prey and coexisting predators.

METHODS

Fieldwork was conducted in the Azores archipelago (37°-40°N, 25°-32°W see Santos et al. 1995 for a description of the archipelago) from 12 to 27 March 1994 and from 28 July to 17 August 1994 (hereafter referred to as March and August, respectively). These dates correspond to the pre-laying and chick rearing periods, respectively (Zino 1971, Granadeiro 1991). On both occasions we collected diet samples in the Central group (Graciosa: Baixo and Praia islets) and Eastern group (Santa Maria: Vila islet). In August the western group was also visited (Corvo; Fig 1).

Cory's shearwaters were captured by hand at their breeding grounds and marked with a metal ring. It was not possible to determine the breeding status of all birds. While in March birds were captured inside and outside burrows, the majority of birds sampled in August were captured when entering burrows to feed their chick.

Diet samples were obtained under licence, by stomach flushing with salt water, by means of a device similar to that used by Wilson (1984) in penguins. Birds were immediately released after being sampled. We did not undertake quantitative validation experiments to assess the effectiveness of the method (e.g. Gales 1987) because excessive disturbance could disrupt breeding (Warham 1990, Granadeiro 1991). Nonetheless, a few trials conducted prior to this study showed that no additional hard remains were obtained when the animals were subjected to a multiple flushing procedure, and therefore no bird was flushed twice. We sampled any individual only once. Some animals had empty stomachs and these were not considered in this study. About 90% of birds caught during the first hour after dark contained food, but this proportion decreased to about 10% of birds caught towards the end of the night, so sampling concentrated on birds arriving early in the night. Food samples were preserved in 70% alcohol, after excess salt water had been discarded. Less than 5% of the samples contained noticeable amounts of stomach oil, and we did not quantify this fraction in this study.

Samples were examined under a binocular microscope and all diagnostic structures were stored dry (fish: otoliths, scales and bones) or in 70% alcohol (cephalopod: beaks, gladii and muscular masses; exoskeletons of crustacea) for later identification. Hard remains were identified using available keys (Nolf 1985, Clarke 1986, Härkönen 1986, Watt et al. 1997) and reference collections of fish bones and otoliths, and squid beaks. For each sample the minimum number of individuals present was determined by the largest number of similar sized/shaped paired structures (fish: otoliths, jaws, cleitra; cephalopods: upper or lower mandibles) or from the number of unpaired remains (fish: spines, vomeric teeth, diagnostic vertebrae; cephalopods: gladii).

Cephalopods were identified from hard structures (beaks and gladii). Beaks can accumulate in the stomach of seabirds (Furness et al. 1984). To avoid overestimating their importance we counted only undigested beaks and muscle masses. Identification was made to the lowest possible taxon, using reference material and available keys (Clarke 1986, Pérez-Gandaras 1986), and cephalopod nomenclature followed Guerra (1992).

Some food samples were relatively well digested, but most remains were still covered by some muscle tissue. In these situations, vertebrae and squid beaks were generally not eroded by physical and chemical erosion. In contrast, very few otoliths could be found, because fish heads were nearly completely digested or were totally absent. The few otoliths found generally showed evidence of chemical abrasion and were used to identify, but not to estimate size or weight of prey.

In order to reconstruct the original dimensions and weight of fish, we used species-specific regression equations relating vertebrae size with fish size and wet weight (Granadeiro & Silva, unpubl. data). These equations were derived from size of vertebrae that could be uniquely identified even if the skeleton was totally disarticulated. Prey fish size and weight estimates were obtained only when these characteristic vertebrae showed no signs of erosion. The two species of Atlantic saury, *Scomberesox saurus* and *Nanichthys simulans*, both occurring in the Azores (Whitehead et al. 1986), could not be distinguished from vertebral features and were pooled (=sauri). We did not have equations relating bone size with sauri dimension or weight, and hence we used vertebrae measurements obtained from only two specimens in our reference collection. We estimated size of sauri in food samples by linear interpolation using measurements of these two specimens, and weight was computed from log transformed values of weight in relation to vertebral size.

The weight of cephalopods was estimated from measurements of rostral length of well preserved beaks, following equations given in Pérez-Gandaras (1986) and Clarke (1986). A specimen with an estimated weight of 589 g (*Histioteuthis dolfleini*) was not considered in the computations of average weight, because most probably it was not consumed as a whole prey item. Crustacea were detected by remains of their exoskeletons, flesh being generally absent. A weight of 2 g was attributed to each crustacean, based on the average weight of *Pasiphaea spp.* caught off the Portuguese coast during 19 research cruises (2.0 ± 0.1 g), carried out between 1990 and 1997 (A.Silva, *personal communication)*. This procedure was unlikely to produce serious bias in the computations, because crustacea represent a negligible proportion of Cory's shearwater diet.

All vertebrae and squid beaks were measured to the nearest 0.02 mm, using a binocular microscope fitted with an eye-piece graticule. In order to obtain the weight contribution of each species in the diet of shearwaters, we multiplied the number of specimens by the species-specific weight, obtained at each site during each period. Unidentified cephalopods were considered to occur according to the frequency distribution obtained from identified remains. Their contribution by weight was calculated by multiplying the number of individuals thought to belong to a given species by the corresponding estimated weight. When weight estimates were not available for a given species, we calculated a weighed average Family-specific weight. Since we could not measure beaks of Alloposidae and Mastigoteuthidae specimens, these were assigned an arbitrary weight corresponding to the average of all cephalopod specimens (72 g).

In order to estimate fish consumption by Cory's shearwater in the Azores, we multiplied the number of individuals of this species thought to occur in the region by their estimated daily energy requirements (DER) and by the proportion of fish found in their diet. Estimated DER was converted to energy intake needs by dividing this amount by energy assimilation efficiency, taken as 80% (Furness 1994, Warham 1996). The Azorean shearwater population was estimated as 70 000 breeding pairs (Hagemeijer & Blair 1997) and pre-breeding age birds were considered to correspond to 70% of the number of breeders (Warham 1996, Furness 1994), giving a total of about 238 000 adults. We did not include consumption by chicks since this represents only about 5-10% that of adult birds (Mougin et al. 1996). In the absence of direct measures of energy expenditure, we estimated DER from published relationships between field metabolic rates (FMR) and bird weight (W) in Procellariiformes: FMR ($KJ.day^{-1}$)=$22.34*W(g)^{0.575}$ (Warham 1996). Species-specific calorific values were not available for most prey items and these are likely to exhibit large variations due to a variety of factors (*e.g.* Hislop et al. 1991). For the purpose of this crude assessment, we adopted an average value of 6 $KJ.g^{-1}$ wet weight, based on values obtained on several fish species (Warham et al. 1976, Clarke & Prince 1980, Hislop et al. 1991). This assumption is likely to produce small errors, compared to those arising due to the imprecision in the shearwater population estimates.

There is still some debate about the taxonomic status of trumpet fish in relation to a possible separation of the forms *Macrorhamphosus scolopax* and *M. gracilis* (Brêthes 1979). Therefore in this study, trumpet fish are referred to as *Macrorhamphosus* sp. Dietary information is presented in terms of frequency of occurrence (% samples with a given prey item), numerical importance (number of specimens of each prey type, expressed as % of all prey found) and proportion by weight (weight contribution of a given species, as % of total weight). Statistical procedures followed Zar (1996). Throughout this paper, we present means ± standard deviation.

RESULTS

Frequency of occurrence and numerical importance of prey

All fish remains found in food samples could be attributed to 5 species/genera (Table 1). Fish was the most important prey type in terms of both occurrence (90.6% in March, 96.2% in August; Table 1) and number (91.9% in March, 95.7% in August; Table 2). There was no significant difference between the two periods in the proportion of samples containing fish (Yates-corrected $\chi^2 = 1.19$, P=0.3, df=1).

In August, boarfish *Capros aper* and trumpet fish dominated the diet in terms of occurrence (Table 1) and numbers (Table 2). Taken together these species were present in more than 85% of the samples and also represented more than 85% of all prey found in this period (Table 2). Boarfish occurred less frequently in diet samples in March as compared to those collected in August (Yates-corrected $\chi^2 = 15.11$, P<0.0001, df=1) and its numerical importance was also lower. In August, trumpet fish were significantly more frequent (in occurrence) in Santa Maria than in Graciosa and Corvo ($\chi^2 = 26.8$, P=0.0001, df=2), while the converse was true for boarfish, which was relatively uncommon in Santa Maria ($\chi^2 = 51.6$, P<0.0001, df=2). There is some suggestion of a similar geographical pattern in March, but the spring sample sizes were too small to enable meaningful statistical analysis.

All cephalopods identified belonged to the Order Teuthoidea, Sub-Order Oegopsida, except one specimen identified as *Halyphron atlanticus* (syn. *Alloposus mollis*), which belongs to the Order Octopoda, Sub-Order Incirrata (Table 3). In both periods slightly eroded structures or muscle were found on about 25% of the samples and their numerical importance varied between 3.0% and 14.3% (Table 3). Histioteuthidae was the most represented Family (3 species, 41.4% by number), followed by Cranchidae (5 species, 27.6% by number) and Gonatidae (1 species, 17.2% by number). All species consumed by shearwaters are mesopelagic, some also presenting epipelagic (especially juvenile forms) or bathypelagic distribution (Table 3). It is worth highlighting that severely eroded squid beaks (usually the tips of lower and upper mandibles) were found in 60.4% and 52.7% of the samples analysed in March and August, respectively, and if considered (see Methods) would have represented *ca.* 10% of all prey found.

Crustacea were represented by few individuals (Table 1). Six specimens were classified as Decapoda Natantia. From these, 3 were identified as *Pasiphaea* sp. Their relatively large size (ca. 5 cm) and low state of digestion suggests that they were not taken by fish or squid species found in samples.

Size of prey and their contribution by weight

Table 4 shows the estimated size and weight of prey fish, obtained from 760 measurements of fish vertebrae. The means presented in Table 4 were calculated from average size/weight of each species in each food sample, to account for potential problems arising due to the effects of pseudoreplication (Hurlbert 1984). There were small but significant differences in size and weight of prey captured in both periods (Table 4). The statistical significance of the comparisons and the magnitude and "direction" of the differences remained unaffected when tests were applied to all measurements obtained from food samples, suggesting that there was no inverse relationship between size and number of fish in our samples.

Estimated weights of cephalopod species are presented in Table 3. Overall, fish contributed about 75% weight and cephalopods 25% (Table 5). Cephalopods were the most important prey in March, followed by sauri (35.7%) and trumpet fish

(17.9%). In August, fish prey were proportionally more important (82.0% in weight), with boarfish contributing 29.4%, followed by sauri, trumpet fish and horse mackerel *Trachurus picturatus*.

Estimates of fish consumption by Cory's shearwaters

Adult Cory's shearwaters in the Azores weigh about 900 g (Granadeiro 1993), yielding an estimated DER of about 1116 $KJ.day^{-1}$ (see Methods). During 270 days, roughly corresponding to their period at the breeding grounds (Zino 1971, Granadeiro 1991), Cory's shearwaters would consume about 11200 tonnes of fish.

DISCUSSION

Diet of Cory's shearwaters

Cory's shearwater is a surface-seizing predator, apparently unable to capture prey deeper than 2 m (Haney 1986, Monteiro et al. 1996a), in contrast with other shearwaters better adapted to diving (Warham 1990). Previous observations of the feeding behaviour of Cory's shearwater have suggested fish and squid to be the main prey (Martin 1986, Monteiro et al. 1996a), either caught alive or through scavenging (Abrams 1983, Sara 1993) occasionally in association with underwater predators such as marine mammals and tuna (Martin 1986).

Our data indicate a predominately fish diet of Cory's shearwater in the Azores, involving few species. Small shoaling fish, mainly trumpet fish and boarfish, were the most frequent prey, presumably caught as they shoaled in large numbers close to the surface. These prey fish mainly include 1-year class (as assessed by their average size, following Brêthes 1979), extremely abundant in the area roughly delimited by the Azores archipelago, the south of Portugal and the Canary islands (Ehrich 1975). However, due to their small size, their contribution by weight is not as high as that of sauri.

Small pelagic fish also formed the basis of the diet of most diurnal feeding seabirds in the Azores. Taken together, boarfish and trumpet fish represented more than 60% of the prey found in pellets or delivered to chicks of common tern *Sterna hirundo* (Granadeiro et al. 1995), roseate tern *Sterna dougalli* (Ramos et al. in press a) and Cory's shearwater (this study). Boarfish and trumpet fish were also present in about 70% of the yellow-legged gull *Larus cachinnans* pellets containing fish (Ramos et al. in press b). There are no estimates of the importance by weight of these two fish prey in the diet of any seabird in the Azores, but given their comparatively higher frequency (Ramos et al in press a, b) they certainly represent a major contribution to their diet by weight.

The importance of boarfish in the diet of Cory's shearwater is somewhat surprising as this species is seldom consumed by seabirds in the Mediterranean, despite being discarded in large numbers during trawling activities (Oro & Ruiz 1997). Experimental fish discards in the Mediterranean also support the view that boarfish is not a preferred prey (Sara 1993), because most seabirds select prey such as European anchovy *Engraulis encrasicolus*, horse mackerel and blue whiting *Micromesistius poutassou*, which are easier to handle and swallow (Sara 1993).

In August, boarfish and trumpet fish exhibited a significant geographical variation in their importance in shearwater diet (Table 1). The former species was found more frequently and contributed more by weight in Corvo and Graciosa, being less common in Santa Maria, while trumpet fish showed the reverse pattern. The proportionally larger importance of trumpet fish in the eastern group is also documented in common terns in the Azores (Granadeiro et al. 1995), which is consistent with the hypothesis that these differences reflect genuine variation in the availability of such prey.

Temporal variation in diet of Cory's shearwater has never been reported and is difficult to interpret in light of current knowledge. The fact that we collected data during only one year precludes assessment of inter-annual consistency of such a pattern. It is not possible to ascertain the extent to which it reflects a change in prey availability, a shift in prey selection, or a change in foraging areas, as breeding season progresses. Indeed, Cory's shearwaters can profit from oceanographic phenomena

such as eddies, and major upwelling events associated with seamounts, known to be related to biomass enhancement (Haney 1986, Rogers 1994). However, the extension and frequency of such phenomena in Azorean waters remains largely unknown and whether the temporal differences found in this study could correspond to varying intensity of such events in different times of year, remains a matter for speculation. Alternatively, temporal differences could be attributed to active prey selectivity. Differences in the food of adult seabirds and that provided to their chicks have been described in some seabird species (*e.g.* Furness & Hislop 1981, Nogales et al. 1995) and interpreted as a means for providing a better quality food to chicks. Squid was equally represented in numbers in both periods (Table 2), but its importance by weight in March was twice that recorded in August (Table 5). The decrease in the proportion of squid (which is of lower calorific value; Warham et al. 1976; Clarke & Prince 1980, Furness 1994) in the diet of shearwaters in August, could therefore reflect an increase in prey selectivity as breeding season progresses, and the subject clearly deserves further investigation.

The frequency of occurrence of cephalopods in the diet of shearwaters agrees with previous data from the Azores presented by Furness (1994), which were used to estimate the amount of squid consumed in this area. This estimate was based on hard remains obtained from stomach-flushed birds, as well as post-mortem analysis of the contents from gizzards of fledglings that had died from accidents, and the vast majority of squid found were identified as Ommastrephids (Furness 1994). The preponderance of this Family has also been reported by Martin (1986), but that contrasts with our findings, which suggest a considerably higher diversity of squid prey (12 species, 6 Families). Our observations highlight the possible role of seabird dietary studies as a means of sampling the marine environment (Furness & Greenwood 1993, Cherel & Weimerskirch 1995, Croxall & Prince 1996, Furness & Camphuysen 1997).

Although juvenile forms of some of the squid species represented show an epipelagic distribution (Clarke 1986), adult animals occur mainly in mesopelagic or even bathypelagic environments (see Table 3). These species undertake diel vertical migrations, ascending to the surface only at night (Imber 1973, Prince & Morgan

1987). Similarly, boarfish and trumpet fish are epipelagic while juveniles, undergoing a shift in their vertical distribution when adults, and occur mainly at 50-150 m and 100-400 m, respectively (Brêthes 1979, Whitehead et al. 1986). Klomp & Furness (1992) suggested that the later arrival of shearwaters at a colony on moonlit nights could indicate enhanced prey availability or visibility, which could explain the presence of these deep water prey in our samples. However, there is little evidence for a relationship between time of arrival and nocturnal feeding at other colonies (e.g. Hamer & Hill 1993, Granadeiro et al. in press), suggesting that mesopelagic prey can be obtained during the day. Although it is likely that shearwaters feed opportunistically at night, most deep water prey are probably driven to the surface by underwater predators, such as tuna and marine mammals (Prince & Morgan 1987, Au & Pitman 1988, Croxall & Prince 1996) or by local upwelling events (Monteiro et al 1996a, Ramos et al. in press a).

While deep water squid species were detected in diet samples, mesopelagic fishes (e.g. Myctophidae, Sterniptychidae or Gonostomatidae) were strikingly absent. These prey are thought to occur in large numbers in the area (Gjøsaeter & Kawaguchi 1980), and therefore represent a potential source of food. These species occur regularly in the diet of Common terns (Granadeiro et al. 1995, Ramos et al. in press b), Roseate tern (Ramos et al. in press a) and of most small petrels breeding in the Azores (Monteiro et al. 1996a, JPG unpubl. data). Their presence has also been reported in Yellow-legged Gull (Hamer et al. 1994, Ramos et al. in press b, JPG unpubl. data). Hence, deep water fishes are readily available to mainly diurnal foraging seabirds, some of which probably sample the environment in much the same way as shearwaters. Since mesopelagic fish usually possess large otoliths (Nolf 1985, Härkönen 1986) and resistant maxillary and teeth (Watt et al. 1997) it is extremely unlikely that if they were present we systematically failed to detect them in all our samples.

The reduced importance of mesopelagic prey in the diet of shearwaters is further supported by the mercury levels in their plumage and food regurgitations. Mesopelagic organisms tend to show high mercury concentrations (Monteiro et al. 1996b) and high mercury levels are also found in seabird species (mainly small

petrels) which rely extensively on these prey, reflecting a causal link between diet and mercury burdens (Monteiro 1996). In contrast to these species, Cory's shearwaters present an overall low mercury burden (Monteiro 1996), which is consistent with the absence of deep water fish species in their diet recorded in this study.

Fish consumption and comparison with other marine predators

Cory's shearwaters were estimated to consume about 11000 tonnes of fish per year in the Azores region. The scarcity of information on fish standing stocks, and on natural and fisheries-induced mortality precludes any assertion about potential competition with local fisheries (Furness 1982, Montevecchi 1993). However, Cory's shearwaters in the Azores feed mainly on non-commercial species and therefore interaction with fisheries, if any, is only likely to occur in relation to horse mackerel, caught to some extent as live bait for local tuna fisheries. In the Azores, Pinho et al. (1995) estimated an annual catch of small horse mackerel of about 305 t and 226 t in 1993 and 1994, respectively, and the sizes taken (80-230 mm fork length) are well within the range captured by shearwaters (Table 4). Assuming that horse mackerel represents 8% (by weight) of the prey taken (Table 5), Cory's shearwater would consume about 1046 t per year, almost an order of magnitude higher than that of bait catches. Horse mackerel can exhibit important inter-annual variations in abundance (Pinho et al. 1995) but the extent to which both commercial catches and natural consumption are likely to be affected is unclear. Cory's shearwater is mainly an opportunistic feeder and therefore it is unlikely that a reduction in a single prey type would significantly affect their provisioning behaviour. Nonetheless, long-term studies of shearwater diet can provide indications on relative abundance of these prey fish, possibly enabling an assessment of their availability in the Azorean pelagic food web.

The diet of Cory's shearwater in the Azores shows several similarities with prey taken by underwater predators. Boarfish was the most commonly found prey in the diet of swordfish *Xiphias gladius* in the Azores (72% occurrence, 76% by

numbers), being the second most important prey by weight (Clarke et al. 1995). The estimated fork length and weight of fish taken by swordfish (70 mm and 5 g, respectively, Clarke et al. 1995), is well within the range captured by shearwaters (Table 4). Similarly, blue sharks *Prionace glauca* examined by Clarke et al. (1996) in the central group of the Azores showed a preponderance of boarfish (49% by numbers and 21% by weight) and trumpet fish (34% in numbers, 21% by weight). The size of intact boar fish peaked at 50-60 mm (Clarke et al. 1996), which is in general agreement with the size consumed by shearwaters, as obtained from fish vertebrae measurements (Table 4).

Further similarities can be seen with data obtained from commercial fisheries in the Azores. Small shoaling species are captured alive to provide bait for tuna fisheries (Pinho et al. 1995). These species include blackspot seabream (*Pagellus bogaraveo*) and horse mackerel, the former not reported in Cory's shearwater diet, as it mainly exhibits a coastal distribution (Whitehead et al. 1986). Bait catches are carried out at night, when individuals are attracted to the surface by intense lights from the boats, and fish are captured using purse-seine nets (Pinho et al. 1995). Modal size for fish captured with this gear are 140 mm (fork length) for horse mackerel and 220 mm (fork length) for chub mackerel *Scomber japonicus*, almost exactly matching our estimated measurements for shearwaters prey (Table 4). The broad similarity in the sizes preyed upon by different predators suggests that they are sampling all available size classes, thus being potentially useful as indicators of the availability of these prey (Furness & Greenwood 1993, Furness & Camphuysen 1997).

These considerations support the notion that small pelagic prey probably occur in very large numbers in Azorean waters. At high latitudes, a single abundant prey supports a wide range of predators: krill in the southern oceans support many species of seabirds, seals and whales (eg Kasamatsu & Joyce 1995, Reid & Arnould 1996, Croxall et al. 1997, and references therein); capelin in the Barents sea supports seabirds, seals and cod (review in Gjøsæter 1997). However, it is generally found that at low latitudes prey species diversity is much higher (Ashmole 1971, Croxall 1987). Yet, in the Azores, only two species of small fish appear to be key prey for a variety of predators. The central role of trumpet fish and boarfish in the marine food web in

the Azores, and the fact that these prey can exhibit strong variation in abundance (e.g. Brêthes 1979) raises the question of how adaptable predators will be to extensive changes in their availability.

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Table 1 - Frequency of occurrence (%) of fish species, cephalopods and crustacea in food samples of Cory's shearwaters in the Azores

	March			August				TOTAL
Species	**Graciosa**	**Sta Maria**	**Total**	**Corvo**	**Graciosa**	**Sta Maria**	**Total**	
Sauri	-	29.8%	26.4%	13.8%	19.0%	11.4%	15.1%	18.9%
Trumpet fish	16.7%	44.7%	41.5%	27.6%	31.0%	82.9%	47.2%	45.3%
Boarfish	50.0%	19.1%	22.6%	69.0%	88.1%	8.6%	56.6%	45.3%
Horse mackerel	16.7%	-	1.9%	13.8%	28.6%	22.9%	22.6%	15.7%
Chub mackerel	-	2.1%	1.9%	6.9%	2.4%	5.7%	4.7%	3.8%
Crustacea	-	12.8%	11.3%	-	4.8%	2.9%	2.8%	5.7%
Cephalopoda	50.0%	21.3%	24.5%	17.2%	19.0%	37.1%	24.5%	24.5%
Number of samples	6	47	53	29	42	35	106	159

Table 2 - Numerical frequency (%) of fish species, cephalopods and crustacea in food samples of Cory's shearwaters in the Azores

	March			August				TOTAL
Species	**Graciosa**	**Sta Maria**	**Total**	**Corvo**	**Graciosa**	**Sta Maria**	**Total**	
Sauri	-	9.6%	8.8%	3.3%	3.0%	3.6%	3.3%	4.7%
Trumpet fish	33.3%	67.0%	64.2%	15.0%	14.0%	77.8%	39.8%	46.0%
Boarfish	47.6%	15.5%	18.1%	70.8%	74.4%	7.2%	46.8%	39.5%
Horse mackerel	4.8%	-	0.4%	5.0%	4.7%	5.2%	5.0%	3.8%
Chub mackerel	-	0.4%	0.4%	1.7%	0.3%	1.0%	0.8%	0.7%
Crustacea	-	2.5%	2.3%	-	0.6%	0.3%	0.4%	0.9%
Cephalopoda	14.3%	5.0%	5.8%	4.2%	3.0%	4.9%	3.9%	4.4%
Number of prey items	21	239	260	120	336	307	763	1023

Table 3 - Cephalopod species identified in Cory's shearwater diet in the Azores in March and August, and corresponding vertical distribution (E - epipelagic, M - mesopelagic, B - bathypelagic, following Clarke 1986, Guerra 1992). Weight (mean ± standard deviation, sample size in parenthesis) was estimated from beak measurements (for explanation, see text).

Family Genus/Species	Vertical distribution	Depth (m)	No of individuals March	 August	TOTAL (%)	Estimated (g)
Ommastraphidae						
Ommastrephes sp.	E,M	0-1500	1	-	2.2%	3.7±0.7 (2)
Gonatidae						
Gonatus steenstrupii	M	0-1000	4	1	11.1%	166.0±136.1
Histioteuthidae						
Histioteuthis sp.	M	-	2	-	4.4%	-
H.reversa	M	0-1800	-	6	13.3%	36.6 (1)
*H.dolfleini**	M	0-700/800	3	-	6.7%	140.3±54.8 (2)
H.maleagroteuthis	M	100-700	-	1	2.2%	-
Mastigoteuthidae						
Mastigoteuthis sp.	M/B		-	2	4.4%	-
Cranchidae						
Cranchia scabra		0-200	-	1	2.2%	-
Leachia sp.	M-B	0-2000	-	4	8.9%	5.3 (1)
Taonius pavo	M-B	0-2000	1	-	2.2%	80.5 (1)
Teuthowenia sp.	E-M	0-1500	1	-	2.2%	-
Galiteuthis sp.	M-B	500-2000	-	1	2.2%	-
Alloposidae						
Halyphron atlanticus	E-M	0-3000	-	1	2.2%	-
Unidentified	-	-	3	13	35.6%	-
TOTAL			15	30		

* one individual with an estimated weight of 589 g excluded from computation on mean weight

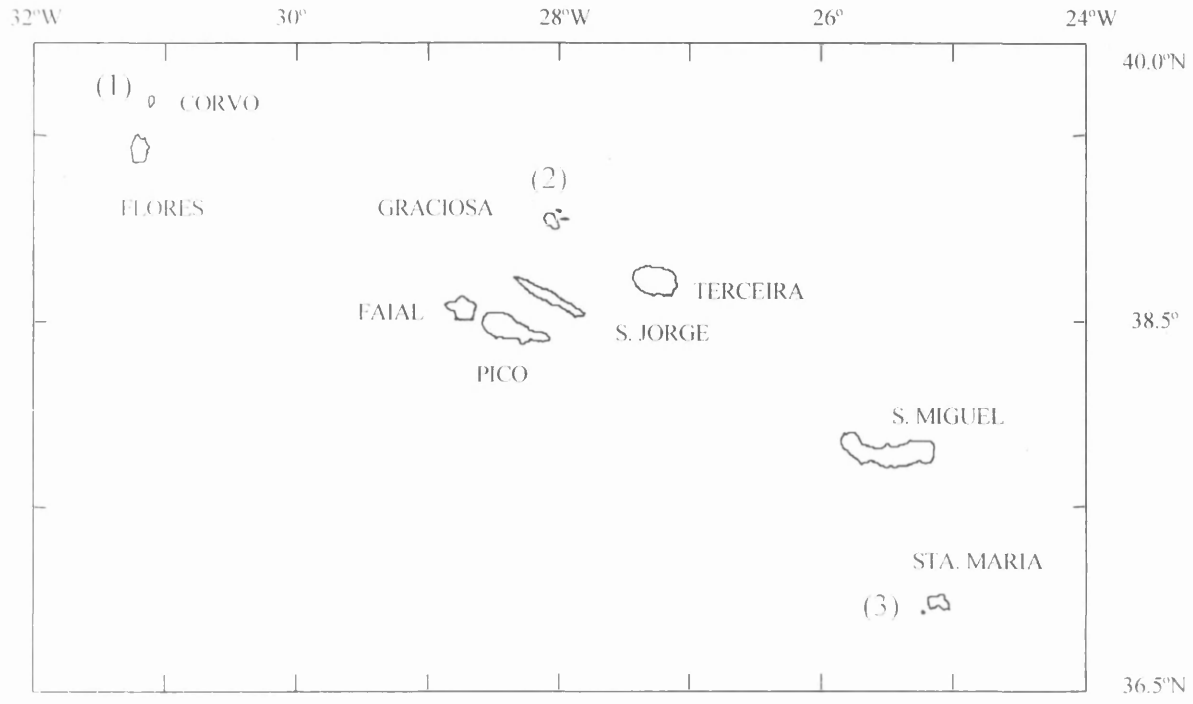
Table 4 - Standard length (boarfish and trumpet, in mm) and total length (all other species, in mm) and weight (g) of fish of Cory's shearwater in the Azores, in March and August, and statistical comparison between months. Means values (± standard deviation, sample size in parenthesis, range below) were estimated from vertebrae measurements, and were calculated as averages per food sample (for explanation, see text).

Species	Vertebrae used in estimations	Fish length (mm)		Fish weight (g)		Mann-Whitney U-test
		March	August	March	August	
Sauri	1st caudal	376.0±12.9 (6) 365.1-397.0	355.3±30.7 (6) 312.5-406.6	69.8±9.31 (6) 62.0-85.0	57.8±19.4 (6) 34.5-93.0	U=6, P<0.05
Trumpet fish	4th,5th,1st caudal	87.4±5.5 (17) 71.9-95.4	82.8±11.2 (26) 68.2-115.8	4.7±0.7 (17) 2.8-5.9	4.2±1.8 (26) 2.4-9.8	Z=2.81, P<0.01
Boarfish	5th, 1stcaudal	61.2±5.3 (6) 57.5-71.4	54.5±4.9 (30) 49.0-70.8	8.9±2.3 (6) 7.5-13.4	6.5±1.9 (30) 4.6-13.4	Z=3.01, P<0.01
Horse mackerel	1st caudal	-	139.1±13.2 (9) 119.9-157.3	-	22.3±6.2 (9) 14.2-30.9	-
Chub mackerel	1st caudal	191.4 (1) -	237.3±68.8 (2) 188.7-286.0	39.6 (1) -	110.1±102.7 (2) 37.0-187.7	-

Table 5 - Importance by weight (%) of fish, cephalopods and crustacea in the diet of Cory's shearwater at each colony, in March and August

Species	March			August				TOTAL
	Graciosa	Sta Maria	Total	Corvo	Graciosa	Sta Maria	Total	
Sauri	-	39.7%	35.7%	18.6%	18.0%	18.0%	18.1%	24.9%
Trumpet fish	7.0%	19.1%	17.9%	7.3%	7.6%	30.8%	16.8%	17.2%
Boarfish	15.8%	7.4%	8.3%	37.1%	49.4%	4.2%	29.4%	21.2%
Horse mackerel	5.0%	-	0.5%	14.4%	9.9%	13.7%	12.2%	7.7%
Chub mackerel	-	1.0%	0.9%	4.9%	1.2%	10.7%	5.6%	3.8%
Crustacea	-	0.3%	0.3%	-	0.1%	0.1%	0.1%	0.2%
Cephalopoda	72.2%	32.5%	36.5%	17.7%	13.7%	22.5%	17.9%	25.1%
Total weight of prey (g)	461	4096	4558	1214	3138	2867	7220	11778

Figure 1 - Location of the study colonies, within the Azorean archipelago. (1) Corvo mainland; (2) Praia and Baixo islets; (3) Vila islet.



Chapter 5

The relationship between mercury levels and diet in azores seabirds

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ABSTRACT

Mercury concentrations were determined in feather and food samples from adults of six seabird species from the Azores archipelago. Mean concentrations ranged from 54 to 432 ppb dw in food and 2.1 to 22.3 ppm fw in feather samples and were highly significantly and positively correlated. Significant seasonal differences in dietary mercury were also registered. Both feather and food mean concentrations were four-fold higher in seabirds feeding on mesopelagic prey than in those feeding predominantly on epipelagic prey. Concentrations in feathers were 150x those in food, which represents the highest methylmercury biomagnification factor reported for consumers in aquatic foodchains. These findings show that the inclusion of mesopelagic prey in seabird diet has an influence on mercury accumulation over and above that from trophic status and emphasises further the value of seabird feathers as monitors of the ecological hazards of mercury in marine ecosystems.

INTRODUCTION

Concentrations of mercury in the environment have increased many-fold since pre-industrial times (Pheiffer-Madsen 1981, Swain et al. 1992, Nater & Grigal 1992, Thompson et al. 1992, Monteiro & Furness 1997) as a result of anthropogenic emissions of gaseous mercury to the atmosphere (Mason et al. 1994, Hudson et al. 1995). The oceans play a major role in the global cycle of mercury (Fitzgerald 1989) and monitoring of the marine environment is a priority (EPMAP 1994). In this respect, biomonitors present good prospects for comprehensive appraisals of the abundance and bioavailability of mercury (Phillips 1980) because marine cycling of this metal includes many biologically-mediated processes (Mason & Fitzgerald 1990, 1993). Seabirds, in particular, have featured prominently as monitors of spatial and temporal patterns of mercury contamination in marine ecosystems based upon a growing knowledge of the metal dynamics in the organism (reviews in Walsh 1990, Furness 1993, Monteiro & Furness 1995).

Mercury dynamics in seabirds is best viewed as a multi-compartment model involving ingestion from diet, uptake in the intestine, transport in blood, accumulation in internal tissues (e.g. muscle, liver, kidney) with redistribution to the plumage during feather growth, and elimination in eggs and excreta. The plumage contains over 70% of the mercury body burden in adults of a variety of bird species, despite forming less than 10% of total body weight (e.g. Braune & Gaskin 1987, Honda et al. 1986). Seabirds usually renew their plumage every year after breeding and then much of the dietary mercury accumulated in soft tissues between moults (most seabirds do not moult feathers over a 5-6 month period; Ginn & Melville 1983) is mobilised into growing feathers. Feathers samples have been widely used for the assessment of whole-bird mercury burdens due to several methodological and conceptual advantages over other tissues: i) feather sampling is easy and relatively non-invasive; ii) mercury is stably bound to feather keratins (Appelquist et al. 1984), thus special preservation procedures are not required and the metal can be determined in historical samples; iii) feathers exhibit high concentrations with minor seasonal variations

(Monteiro 1996); iv) concentrations in feathers correlate positively with those in internal tissues (Thompson et al. 1991, Lewis & Furness 1991); v) feather concentrations integrate mostly the uptake and storage of mercury during the breeding season, rather than short-term uptake (Furness et al. 1986, Honda et al. 1986, Braune & Gaskin 1987).

Large variations in mercury levels among seabird species have been documented and attributed to a variety of proximate and ultimate factors such as trophic level, migratory habits, body size, life span, moult pattern and taxonomic influences on physiology (Walsh 1990, Monteiro & Furness 1995). Dietary and feeding differences have been proposed as the best explanation for consistently low mercury levels in those species which feed predominantly upon crustaceans compared to fish- and squid-eating species (Braune 1987, Honda et al. 1990, Lock et al. 1992); species feeding on other seabirds present some of the highest levels (Stewart et al. 1997). Moult-related constraints in mercury elimination to the plumage seem to increase mercury levels in species with longer than annual moult cycles, like some albatrosses (Furness et al. 1986, Honda et al. 1990). Migratory habits might account for mercury levels in populations subjected to major differences in dietary mercury loadings in breeding and non-breeding grounds (Leonzio et al. 1986). Adult body-size and life-span seem to have irrelevant contributions to mercury levels of adults in species so far studied, as size-dependency or age-related variations are lacking (e.g. Thompson et al. 1991, Burger et al. 1994). Potential taxonomic influences on physiology and mercury dynamics also seem to be unimportant in determining seabirds' mercury levels (Lock et al. 1992, Monteiro 1996). Besides all these factors, major inter-specific differences in mercury levels among fish- and squid-eating seabirds, notably high levels observed in some species at remote oceanic sites, are still poorly understood (Muirhead & Furness 1988, Elliot et al. 1992, Monteiro et al. 1995). The elucidation of such differences is hampered by a major lack of information on mercury levels in seabirds' diet.

Ecological segregation in seabird communities may result in feeding specialisation of some species on epipelagic prey (daytime depth <200m) and of others on mesopelagic prey (daytime depth >200 but migrating into epipelagic zone at

night). Besides, increased concentrations of methylated mercury in seawater below the thermocline (Mason & Fitzgerald 1990) result in enhanced bioaccumulation of mercury in mesopelagic organisms (Monteiro et al. 1996a). Hence, there is a rationale to hypothesise that major inter-specific differences in mercury levels among seabirds may be related to the relative importance of epipelagic and mesopelagic prey in their diet. To test this, we present here a comparison of mercury levels in diet and plumage in six seabirds from the Azores seabird assemblage. Such comparison also provides a quantitative empirical appraisal of a dose-response relationship for mercury in wild birds.

MATERIALS AND METHODS

The study-seabirds were selected according to their predominant dietary and feeding characteristics (Monteiro et al. 1996b, Prince & Morgan 1987) in order to represent two dichotomous groups, one exploiting mesopelagic prey -Bulwer's petrel *Bulweria bulwerii*, Hot-season Madeiran storm petrel *Oceanodroma castro* and Cool-season Madeiran storm petrel (these two temporally segregated storm petrel forms are treated here as sibling species; Monteiro & Furness in press)-, and another exploiting epipelagic prey -Cory's shearwater *Calonectris diomedea borealis*, Little shearwater *Puffinus assimilis baroli* and Common tern *Sterna hirundo*.

Feather sampling was undertaken between April 1993 and June 1995 at three multispecific seabird colonies (Vila, Praia and Baixo Islets) in the Azores (36-39°N, 25-31°W). Food samples were collected between March 1994 and January 1995 in the same seabird colonies as feather samples, except for some regurgitations of Cory's shearwater collected in Corvo island (July, n=29). Sampling was developed conforming to current guidelines for use of wild birds in research and under appropriate licenses from local authorities. Birds were captured by hand on the ground (Cory's shearwater) or using mist-nets (petrels and Little shearwater) and nest traps (Common tern).

Contour feathers are the most representative for estimating whole-plumage mercury concentration in birds (Furness et al. 1986) and up to 10 ventral feathers

were plucked from each of live adults and placed in polyethylene bags prior to analysis for total mercury. For Common tern, diet composition was studied using pellets (made of undigested fish-bones regurgitated by adults and large chicks) and an estimate of food mercury concentration was derived from diet composition (Granadeiro et al. 1995) and mercury levels in prey fish (Monteiro et al. 1996a). Food samples of petrels and shearwaters consisted of spontaneous or induced regurgitations. Regurgitations were obtained from adults during the chick rearing periods (Monteiro et al. 1996b), except for some samples from Cory's shearwater collected in March and all samples from Little shearwater that were collected in September-October. Induced regurgitations were obtained using a stomach-pump (for Cory's shearwater) or a 50 ml syringe (for Little shearwater and the petrels), salt water and a catheter adequate to species size (Wilson 1984, Gales 1985). After examination for the presence of fish, squid or crustaceans, the excess salt water was removed and all solid remains preserved in 70% alcohol for later analysis. In the laboratory, the solid fraction was examined under a microscope and all diagnosing hard parts (otholits, vertebrae, opercular, maxillary and pre-maxillary bones, cleitra, squid beaks, among others) were collected for identification of the prey species. When available, the edible component (hereafter designated as food, made mainly of muscle and accounting for over 80% of the whole net mass) was dehydrated to a constant weight in an oven at 50°C, homogenised using a pestle and mortar and stored in air-tight polystyrene containers until analysis for total mercury.

Sample digestion and total mercury determination follow procedures described in detail elsewhere (Monteiro et al. 1995). Determinations were made by cold vapour atomic absorption spectrophotometry with a Perkin-Elmer Mercury Analyser System Coleman 50B. The limit of detection of the method, taken as twice the standard deviation of triplicate analysis at blank concentrations (Saltzman et al. 1983), was 10 ng, equivalent to 10 ng/g for a 1 g sample. Within- and between-laboratory quality control procedures were employed throughout the study period. Accuracy of the method (expressed as relative error) was within 10% and monitored throughout the study with standards of inorganic mercury, reference materials (NRCC dogfish muscle DORM 1) and participation in the hair mercury interlaboratory

comparison program undertaken by Health and Welfare Canada. Precision (or reproducibility) of the method (expressed as coefficient of variation) of duplicates within and between batch was generally within the usual 10% for total mercury determinations in biological samples (Saltzman et al. 1983). Interference on sensitivity due to matrix and pre-treatment were assessed by the method of standard additions before the wet mineralisation digestion. Recoveries of added inorganic mercury averaged 99.8% (S.E.=5.6, n=8) for feather samples and 69.3% (S.E.=6.7, n=8) for food samples. The mean recovery in the food samples differed significantly from 100% (two-tailed t-test for comparison with a hypothesised mean of 100%: t_7=4.58, P<0.005) and all food concentrations were corrected by this factor (i.e. multiplied by 1.44). Mercury concentrations are given in microgram per gram on a fresh weight basis for feather samples (ppm, fw) and nanogram per gram on a dry weight basis (ppb, dw) for food samples. Concentrations in food may be converted to a fresh weight basis using as reference an overall average percentage of moisture in whole fish of 68.8% (S.E.=0.5%, n=95). Potential bias of mercury concentrations in regurgitations related with preservation in alcohol at 70% is assumed to be negligible based on testing with whole-fish reported elsewhere (Monteiro et al. 1996a).

Statistical analysis followed standard procedures (Zar 1984). Data were tested for goodness of fit to a normal distribution using Kolmogorov-Smirnov one-sample test and requirements of homogeneity of variances were determined using Levene test. Where appropriate, parametric or non-parametric tests were employed.

RESULTS

A summary of diet composition of the study-seabirds is shown in Table 1. These data validate the *a priori* separation into two groups based on the predominant origin of their prey, with the petrels exploiting mesopelagic prey and the shearwaters and the tern exploiting mostly epipelagic prey.

Mean mercury concentrations ranged from 54 to 432 ppb dw in food and from 2.1 to 22.3 ppm fw in breast feathers of the six study-seabirds (Table 2). Mercury

levels increase by about four-fold, in both food and feathers, from seabirds feeding in epipelagic prey to those feeding in mesopelagic prey.

Mercury concentrations in food samples of Cory's shearwater were highly significantly different (Mann-Whitney, $Z=5.77$, $P<0.0001$) in the two periods considered (median, range): courtship/March (306, 136-721, n=17) and chick-rearing/July-August (48, 13-329, n=51). Mercury concentrations in food samples of the Hot-season (August) and Cool-season (December, January) Madeiran storm petrels (see Table 2) were significantly different (t-test, $t_{40}=2.20$, $P<0.05$).

Mean mercury concentrations in feathers (ppm fw) and food (ppb dw) were highly significantly and positively correlated ($r=0.968$, $F_{1,5}=73.6$, $P<0.001$). The relationship is described by the linear equation, constrained to pass through the origin (Fig. 1),

$$\text{Hg in feathers} = 0.0493 \pm 0.0057\text{S.E.} * \text{Hg in food}$$

The slope of the former equation represents a food:feather biomagnification factor and assumes the value of 158 ±18S.E. when both concentrations are expressed in ppm fw. Biomagnification factors for each species (Table 2), derived from the ratio of average mercury concentrations in feathers (ppm fw) and food (expressed in ppm, fw; based on a fraction of moisture in fish of 0.688, Monteiro et al. 1996a), have an overall average of 149 (S.E.=15, n=6). These figures represent conservative estimates because food samples analysed for mercury excluded hard parts (fish otholits and bones, squid beaks), presumed to contain no mercury and accounting for ca. 20% of the whole regurgitation net mass.

DISCUSSION

This study provides clear evidence of a direct relationship between mercury in diet and seabirds' mercury levels. The observed inter-species variation of plumage mercury concentrations is not attributable to differences in trophic level, as all the selected seabirds feed predominantly on fish and/or squid and are essentially third order consumers in their food chains. The operational link between mercury in diet

and seabirds' levels appears to be the dichotomy arising from the predominance of epipelagic or mesopelagic prey in the diet. Indeed, average mercury concentrations in breast feathers of seabirds feeding predominantly on epipelagic prey range from 2.1 to 5.4 ppm fw while those of seabirds feeding predominantly on mesopelagic prey range from 11.1 to 22.3 ppm fw. Such enhanced bioaccumulation of mercury by seabirds specialised on mesopelagic prey matches closely the four-fold increase in mercury concentrations from epipelagic to mesopelagic fish preyed upon by seabirds (Monteiro et al. 1996a,b). These findings suggest that high mercury levels found in most petrels from remote locations (Muirhead & Furness 1988, Honda et al. 1990, Lock et al. 1992, Monteiro et al. 1995) derive mainly from specialisation in exploiting diel vertically migratory mesopelagic prey (Prince & Morgan 1987). Hence, feeding specialisation emerges as a major proximate source of inter-species variation of mercury levels among fish- and squid-eating seabirds and presumably other marine predators.

The large seasonal differences of mercury concentrations observed in food samples of Cory's shearwater indicate important seasonal variations in diet composition. Indeed, variations in the frequencies of occurrence of major prey in Cory's shearwater regurgitations were detected between March and July/August, notably a decrease from 36.5% to 17.9% in the importance (by weight) of mesopelagic cephalopods (Granadeiro unpubl. data). However, a poor knowledge of mercury concentrations in prey organisms makes difficult the elucidation of the relationship between the observed seasonal variations in diet and dietary mercury concentrations. The observed mercury enrichment in March food samples may reflect feeding to a greater extent upon prey of mesopelagic origin and/or older fish, both presumed to have enhanced mercury levels (Monteiro et al. 1996a). Indeed, in March the period of darkness is longer than in summer. Therefore, diel vertically migrating mesopelagic prey will be available at surface for longer (Roe & Badcock 1984, Perissinoto & McQuaid 1992). Furthermore, the abundance of age 0 fish increases towards July/August for some prey species (Pinho et al. 1995). Important intra-specific seasonal dietary shifts have been observed in other procellariiforms (e.g.

Thompson & Furness 1995, Warham 1996) and more research on this topic is warranted for the Cory's shearwater.

Differences in mercury concentrations between the two storm petrel forms is mirrored in food, feathers (this study) and eggs (Monteiro 1996), suggesting a noticeable variation in the consumption of mesopelagic prey, which appears to be more important for the Cool-season form. Though full elucidation of this hypothesis is hampered by the lack of detailed dietary information, it conveys new insights into the understanding of ecological isolation between these two presumed sibling species (Monteiro & Furness in press).

The high mercury levels found in the seabirds exploiting mesopelagic prey raise questions about its potential toxicity to those species, especially in view of rapidly increasing mercury contamination in the deep-sea (Monteiro & Furness 1997). Exposure levels inferred from mercury concentrations in food of adult seabirds obtained in this study (means up to 432 ppb dw) are well below the maximum reported avian non-observed-adverse-effect-level (NOAEL) for external symptoms observed in adult Zebra finches *Poephila guttata* subjected to a mercury dietary level of 2.5 ppm dw during 77 days (Scheuhammer 1988). Moreover, exposure levels observed in this study were also below the lowest-observed-adverse-effect-level (LOAEL) in wild bird populations (Thompson 1996), consisting of egg laying and territorial fidelity impairment in Loons *Gavia immer* at mercury concentrations of 0.3-0.4 ppm fw in their prey (Barr 1986). Birds in general exhibit a relatively low susceptibility to methylmercury toxicity. This may result from the remarkable selectivity of methylmercury to the higher and evolutionary more recent structures of the brain such as the cortical areas. Indeed, vulnerability to methylmercury may not have been a problem throughout most of evolution, until recent times when the brain developed in mammals and especially primates (Clarkson 1994). Besides, naturally high exposure of seabirds to mercury in the food chain may have led to the evolution of detoxification mechanisms in these birds related to co-accumulation of selenium (Scheuhammer 1988, Muirhead & Furness 1988).

The findings from this study contribute new insights into the potential of seabirds as monitors for mercury. First, mercury biomagnification (i.e. increase with

trophic levels) high in the food chains involves primarily bioaccumulation of methylmercury (Riisgård & Hansen 1990, Mason et al. 1995) and, in this respect, data presented here constitute the first quantitative field assessment of methylmercury enrichment associated with trophic transfer between fish/squid and seabirds. Because virtually all mercury in fish and bird feathers is methylmercury (>95%; Bloom 1992, Thompson & Furness 1989), the ratios of average feather:food total mercury concentrations indicate an average methylmercury enrichment factor over 150x, while typical enrichment factors observed in field studies with zooplankton and fish muscle, including top predators, are of 2-10x (Windom et al. 1976, Watras & Bloom 1992, Monteiro unpubl. data). This emphasises further the value of seabirds as monitors for mercury and particularly of bird feathers as monitoring units (cf. Furness et al. 1986). Second, ecological segregation in seabird communities has resulted in many parts of the world into feeding specialisation on epipelagic or mesopelagic organisms, especially among procellariiforms (Prince & Morgan 1987). This offers an unique opportunity for easy and inexpensive monitoring of geographical and historical variations in mercury contamination within and between these vertical compartments of marine ecosystems (Monteiro & Furness 1997).

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TABLE 1. - Diet composition for some seabirds at the Azores archipelago. Species codes are the initials of scientific names given in Table 2. Food origin is categorised as epipelagic (E, 0-200 m), epipelagic to mesopelagic (EM, 0-400 m) or mesopelagic (M, 200-1000 m). The frequency of occurrence of food types is scored: absent (0); 1-10% (1); 11-40% (2); >40% (3). Information derived from pellets for the Common tern (Granadeiro et al. 1995) and from regurgitations for other species.

Diet composition		Seabird species (n)					
Food type	Origin	BB (21)	OC-H (39)	OC-C (11)	CD (159)	PA (10)	SH (146)
Fish							
Macroramphosus scolopax	E				3		3
Capros aper	EM				3		1
Trachurus picturatus	EM				2		1
Scomberesox saurus	E				2		0
other epipelagic fish	E				1	3	1
lanternfish[a]	M	3	3	3	0	0	1
Cephalopods	E, M	1	1	1	2	1	0
Crustaceans	E, M	1	1	1	1	0	0

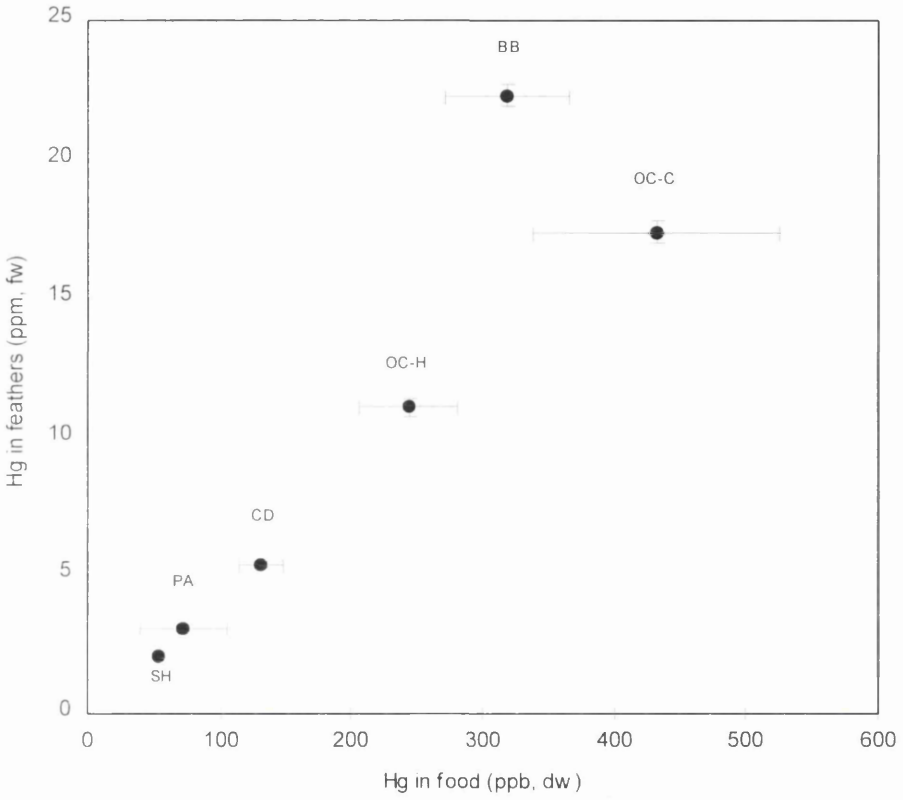
[a] Mostly Myctophidae and Sternoptychidae.

TABLE 2. - Mercury concentrations in food and feather samples of some seabirds from the Azores Archipelago. Values are mean ±S.E., sample size bracketed and range below. See results for definition of biomagnification factor.

Species	Food (ppb, dw)	Breast feathers (ppm, fw)	Biomagnification factor
Bulweria bulwerii	318 ±47(15) 43-738	22.3 ±0.4 (91) 13.8-32.8	225
Oceanodroma castro Hot season	243 ±37 (33) 22-879	11.1 ±0.3 (100) 5.4-23.0	146
Oceanodroma castro Cool season	432 ±94 (9) 128-938[a]	17.4 ±0.4 (130) 6.8-34.3	129
Calonectris diomedea	131 ±17 (68) [b] 13-722	5.4 ±0.1 (186) 1.9-10.4	132
Puffinus assimilis	72 ±33 (3) 27-136	3.1 ±0.1 (82) 1.5-6.9	138
Sterna hirundo	54[c]	2.1 ±0.1 (27) 1.2-3.5	125

[a] Outlier of 2352 ppb dw excluded (> 3rd quartile+1.5 x interquartile range) [b] Simple mean of pooled data from the chick-rearing (July/August) and courtship (March) periods (cf. Methods and Results).[c] Ponderal mean based on frequency of prey fish in diet (Granadeiro et al. 1995) and their mercury concentrations (Monteiro et al. 1996a).

Fig.1 - Relationship between mean mercury concentrations in food and breast feathers of selected seabirds from the Azores. Species codes are the initials of scientific names in Table 2 and standard error are indicated.



Chapter 6

Patterns of activity and burrow attendance in Cory's Shearwater *Calonectris diomedea* as revealed by a novel logging technique

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We monitored the attendance and activity of Cory's Shearwater *Calonectris diomedea* on Berlenga Island, Portugal, during the breeding season. To achieve this, we developed a novel logging technique to record the date and time of entrances and departures from the burrows, as well as the identity of each member of a pair. The technique enables non-intrusive assessment of the activity of burrow-nesting animals over prolonged periods and provided very reliable information. Our study showed that males attended the nests more frequently than females during the pre-laying and chick-rearing periods. We did not find such differences during the incubation period, and both members spent similar amounts of time incubating the eggs. An index of activity (defined as number of entrances plus exits from the nest) achieved higher scores during the pre-laying and incubation periods, but the activity decreased significantly during the chick-rearing period. We did not find any effect of moonlight on the levels of activity, hour of arrival at the colony or time spent inside the burrows in breeding birds.

Procellariiform species have long breeding cycles, as compared with similar-sized birds (Warham 1990). Moreover, 75% of species nest in burrows, caves or rock crevices and although many tend to form dense colonies, most come ashore only at night and are sensitivite to disturbance (K. Thompson, 1987, unpublished PhD thesis, University of Glasgow, Warham 1990), so that studies on their time-activity budgets are difficult.

Although direct assessment of the behaviour of birds once ashore is possible by using especially designed equipment (*e.g.* light intensifiers, infra-red sensitive video-cameras), it still involves demanding observational procedures over long periods of time. This has encouraged the development of devices capable of monitoring the activity of several birds (generally at their nests) and consequently allowing inferences about their behaviour on land. Several designs have been proposed including mechanical nest attendance detectors (*e.g.* Davis 1957, Schramm 1983), electric/electronic balances (*e.g.* Sibly & McCleery 1980, Prince & Walton 1984, Mallory & Weatherhead 1992), electronic event-recorders (Simons 1981, 1985, Ainley *et al.* 1990) and video-camera systems installed inside or outside the burrows (*e.g.* Simons 1981, 1985, Sykes *et al.* 1995). However, while electronic balances and video-camera systems can provide detailed information on bird behaviour, monitoring several nests can be relatively expensive. On the other hand, mechanical systems generally require frequent maintenance (cleaning the mechanisms or contacts, changing recording paper (see Davis (1957) and Schramm (1983))) and birds can not be identified individually. Existing electronic event-recorders overcome most of these problems but fail to discriminate between birds of a pair (Simons 1981, 1985, Ainley *et al.* 1990).

Cory's Shearwaters *Calonectris diomedea* breed in the northeast Atlantic (Madeira, Azores and Canary archipelagos and off the Portuguese mainland coast), in the Mediterranean and in Cape Verde (Cramp & Simmons 1977). Although on Selvagem Grande (about 150 km south of Madeira island) the birds come ashore before sunset (Zino 1971), they only come ashore during the night at all other locations. Several studies have addressed problems related to behaviour at their breeding grounds. Among others, these include work on colony attendance (Mougin *et al.* 1986, Jouanin *et al.*

1989), vocal behaviour and sensitivity to moonlight (Bretagnolle 1990, Bretagnolle & Lequette 1990), patterns of arrival at the colony (Hamer & Read 1987) and food provisioning to the chicks (Klomp & Furness 1992, Hamer & Hill 1993). However, these studies were conducted over relatively limited periods and generalising for broader periods is not possible. We developed an automatic nest-visit recorder which enabled continuous surveillance of the date and time of each entrance and exit for males and females separately from a number of nests. In this paper, we present details of this novel logging system and describe the patterns of activity of Cory's Shearwaters on Berlenga, a small island off the Portuguese coast. We examine differences in the attendance profiles, incubation routines and levels of activity of males and females during the breeding season, and also the extent to which their activity is affected by the levels of ambient light.

METHODS

Design of the Detection System

In order to detect the presence of birds at nests we developed an automatic event recorder which enabled simultaneous logging of activity of several birds over long periods. The system was designed (1) to identify arrival and departure from nests, (2) to record the date and time of each movement and (3) to distinguish between movements performed by each member of a pair.

The monitoring system depends only on the attachment of a correctly oriented (see below) small magnet to each bird. No further disturbance of the birds is required, because there is no energy source to become depleted. The unique property of this system is that the energy for detection is provided by the movement of each bird through detecting coils placed around the nest entrance tunnel. The movement of the magnet induces a voltage in the coils which is analysed and interpreted by the logging system. This system consists of the following parts:

Detection Units

PVC tubes (16 cm internal diameter) were equipped with two coils about 8 cm apart, each wound on the external face of the tube (600 turns, 0.3 mm diameter enamelled copper wire). To avoid birds slipping in the tubes, we lined the surface with cement, glue and sand or simply scored the plastic wall. These tubes were placed at the entrance of the burrows and covered with plastic and rocks. This provided adequate camouflage, protection against heavy rain and excess dust, and also ensured physical stability of the unit. In the few burrows which had multiple entrances, we blocked alternative passages so that access to the nests by shearwaters was only possible through the tube.

Each bird was equipped with a small cylindrical magnet (30 mm long, 3 mm diameter, weighing less than 1 gram), fixed to the base of a central rectrix, using gel super-glue and cloth-backed tape, and longitudinally oriented. When the passage of the magnet induced an electrical signal in each coil, the sequence of activation of the coils was used to determine the direction of movement. If the movement of the bird was fairly uniform the signal induced in each coil was nearly sinusoidal (see Fig. 1), resulting from the passage of a complete north-south dipole through the coil. Opposite orientations of the magnet induced inverse-shaped signals (voltage up then down *v* voltage down then up in both coils, see Fig. 1), and this was used to discriminate between mates.

Amplification

Each tube was equipped with an amplifier board enclosed in a small case (about 5 x 5 x 2 cm), connected to both coils and supplied with 12 v through the 4-way shielded cable from the processing unit. The output signals were referred to a 5 v source on the board, so that regulation of the supply was not needed. Each channel on the board uses a chopper-stabilised operational amplifier for DC stability and provides a gain of about 30,000. Each also has a low-pass characteristic to provide some integration of the signal, so greatly reducing the dependence of the signal on the speed of movement of

the bird through the tube. This characteristic is also needed to prevent pickup of external radio frequency fields.

Processing Unit

This was a microprocessor scanner which can monitor the signals from up to 16 nests. The signals from the units were sequentially sampled by a 16-way differential analog multiplexor and compared with a 5 v reference. If the voltage differred from 5 v by more than a preset threshold, indicating the approach of a bird with a magnet, the scan was halted at that nest until the signals from both coils had been below threshold for 5-s. The threshold (0-2.5 v) could be adjusted to act as a filter against ambient noise or signals generated by birds moving near the coils. Additional features of the scanner included the temporary lock out of channels that remained active for more than 20 s. This prevented the possibility of blocking the sequential surveillance of the nests for extended periods, resulting from technical problems on one coil or amplifier, or from prolonged activity of study birds inside or near the PVC tubes.

The microprocessor encoded the sequence of coil voltages (transitions through threshold) into a sequence of ASCII coded characters. Different characters were assigned to each coil, polarity and direction of crossing through the threshold (*e.g.* positive from 5 v is A in coil 1 and C in coil 2 - see Fig. 1). Additional characters identified the scanner channel (*i.e.* nest) and the end of the 5-s lock time. The characters were sent as RS232 serial data to the storage unit.

Storage Unit

A Psion Organiser II fitted with a Comms Link was selected as a uniquely economical device to interpret and store the data. This device was programmed to add the date and time of each sequence of characters and to store the complete sequence in a data file on an attached Flash RAM pack (128 Kb). A complete event included nest identification, date and time, letter sequence (movement coding) and again the nest number, as an

ending code. The organiser also provided the facilities needed to download the complete data file to a computer for analysis, using the Psion Comms Link (through the RS232 serial connection). The RAM pack had the capacity of storing approximately 4000 average events, i.e. about 2 months of continuous recording (assuming an average of about 60 events per night, see Results). The system was powered by a 12 v car-battery and consumed about 1.6 W with 16 detectors connected (full capacity).

Fieldwork was conducted at Berlenga island, Portugal (39°24'N, 9°30'W) between early April and late September 1996. Both birds from each burrow were caught before egg laying, sexed (on the basis of vocal behaviour or using a classification function based on morphometrics (Granadeiro 1993)), and ringed or identified if previously marked. Birds were then fitted with a magnet on a central tail feather. Males and females were also marked with a different colour spot on the forehead to allow subsequent identification at the nest without any manipulation. No birds were handled during incubation, as they are sensitive to disturbance at that period.

Polarity of magnets deployed on males was opposite to that of females on all pairs, and so generated distinctive signals in the tubes. A few magnets were subsequently lost, mainly due to moult of tail feathers (at the end of the breeding season) and in two cases to feather breakage. The data from the logging system were systematically checked for regularity of the visits of marked birds. Direct capture attempts were undertaken when birds failed to produce signals over prolonged periods. Birds that lost their magnets and were subsequently captured and equipped with new ones were excluded from all the analyses for the period between the day when contact was lost and the date of recapture.

The attachment procedure took less than 3-min and induced no noticeable reaction in terms of the birds' behaviour. A few birds were captured while feeding their chick at the burrow. After handling they were re-introduced through the tubes and none seemed unduly disturbed by the attachment procedure and most of them continued feeding their chick.

The first detection units were installed on 18 April (10 units) and new tubes were subsequently added as new pairs were equipped with magnets. The number of birds equipped with magnets in monitored burrows varied between 12 and 32 during the study period. Between 6 and 16 nests (the maximum capacity of the system) were simultaneously monitored.

Cory's Shearwaters show high fidelity to site and mate (Mougin *et al.* 1987, Thibault 1994) and so attempts were made to catch birds in burrows (thought to represent breeding birds), and the identity of each member of the pair was checked against information from pair bonds in previous years. Three pairs initially selected for monitoring did not produce eggs or lost it during incubation and data gathered from these nests were excluded from further analysis. New pairs were subsequently selected as soon as the reproductive failure was detected and all data in the paper refer to successful breeders.

Laying and hatching dates were not assessed for all nests. Cory's Shearwaters start laying by the end of May (Zino 1971, Zino *et al.* 1987, Granadeiro 1991). By 4 June all monitored nests were occupied by incubating birds, and this date was considered to separate the pre-laying from the incubation period. Similarly, on 25 July, all the nests with tubes had small chicks (most of them still brooded by one of the parents), and this date was considered to be the start of the chick-rearing period. These dates match well with information from previous years which also showed that laying and hatching tend to be highly synchronised (Granadeiro 1991; JPG personal observations). Chicks tend to leave the nest by the end of October at an average age of 95 days (Granadeiro 1991), but this paper only contains data up to 15 September.

Statistical analyses

Our data represent repeated measures over several days from the same individuals. These data are not independent and we calculated test statistics over means for individual birds or nests as appropriate, following Zar (1996). Data were checked for

normality and homogeneity of variance prior to the application of parametric statistical tests. Yates' correction for continuity was used where adequate, following Zar (1996). Throughout this paper we present means±standard deviation, except where otherwise stated.

RESULTS

Reliability of the detection system

Between 1 May and 15 September, 7721 movements were recorded over a period of 125 days. The system failed on 13 days due to short-circuits caused by Black Rats *Rattus rattus* chewing cables (11 days) or a system breakdown provoked by a failure of an amplifier exposed to high voltage (2 days). Subsequent protection of the cables with hard plastic tubing prevented damage by rats, desiccation by the sun and general physical damage.

During a single night an adult often entered and left the burrow several times so several "paired movements" (logged entrance plus exit) occurred per visit. The fact that the scanner locked onto an active channel (nest) implied that simultaneous movements at other nests could have occurred and failed to be detected by the system. This limitation resulted in "unpaired movements" being recorded, *i.e.* double entrances without an intermediate exit (or *vice-versa*).

To assess the extent to which these situations affected the reliability of the system, we estimated (1) the number of times we failed to detect both an entrance and an exit (missing two "single movements"), and (2) the number of times that birds visited nests and all their movements failed to be recorded (missing attendance). First, we analysed the probability of missing a single movements (entrance or exit) by assuming that entrances and exits were occurring independently. We denoted the probability of missing a single movement as q and recording it as $(1-q)$. Failed entrances and exits occurred with the same frequency (132 out of 3861 *v* 138 out of 3860, respectively; χ_1^2

= 0.09, n.s.). Because the probability of simultaneously missing two single movements (q^2) could not be computed directly, we estimated q by matching the number of paired movements $(N*(1-q)^2)$ against the number of unpaired movements $(N*2q(1-q))$, using the total number of events (N - see Table 1) as a linking value. This resulted in the expression:

$$q = \frac{\text{Number of unpaired movements}}{[(2 \times \text{Number of paired movements}) + \text{Number of unpaired movements}]}$$

Most birds performed more than two single movements each night (see below) and so the probability of completely missing the presence of a bird at the nest in any night was computed as the probability of missing two single movements (q^2) raised to a power equal to the average number of movements per bird and per day.

Table 1 shows the details of these computations for three phases of the breeding cycles and also for the whole period. The probability of missing two single movements was highest during the chick-rearing period, because the high attendance values (see below) compensated for the decrease in the overall activity. Moreover, during this period the number of birds carrying magnets reached its maximum (average = 29 birds) and so the total number of recorded movements was higher during this period and consequently the probability of occurring simultaneous movements.

We estimate that the system failed to detect two consecutive single movements on only five occasions (entrance plus exit or *vice versa*) and that virtually no birds visited the nest without being detected (Table 1). During the pre-laying and incubation periods, nests were irregularly checked for occupancy and the sexes of birds were verified against data from the loggers. In no situation did we record discrepancies between observed and recorded sexes (n = 141 bird-days). Additionally, between 1 and 11 August, 15 chicks from monitored burrows were periodically weighed during the night. On no occasion did we record an increase in the weight of chicks without a

corresponding record of movement from at least one adult. Moreover, all occasional observations of adults at the nest during the weighing procedure had a corresponding record on the detection data file. These periodic weighings were repeated between 9 and 25 September (240 chick-nights) and again no discrepancies were observed. From this, we are confident that the system logged all attendances by the marked adults while it was operational.

Attendance patterns

Figure 2 shows the attendance patterns of male and female Cory's Shearwaters during the breeding season (attendance was expressed as the proportion of birds carrying magnets that visited the nests each night). Males showed highest attendance in the first two weeks of May, and the lowest values for females occurred about one week later. During the pre-laying period, males attended the nest more frequently than did females (males: 0.728 ± 0.168 night^{-1}, n = 12; females: 0.145 ± 0.086 night^{-1}, n = 12, paired t-test, t_{11} = 11.2, $P < 0.0001$). Our data indicate that females undertook a pre-laying exodus which lasted for about 3 weeks, while males decreased their attendance at the colony about six days before the start of laying (first eggs in the last week of May), but never reached the low attendance levels recorded for females.

In the early stage of incubation, patterns of attendance closely reflected the regular alternation of incubation shifts (Fig. 2). In order to compare the incubation routines of males and females, we only considered the period between 4 June (when all eggs were known to have been laid) and 15 July (484 nest-nights) to prevent the possibility of including nests where chicks had already hatched. In this period, there were no differences between sexes in the time spent incubating (males: 51.6% ± 6.8%, n = 14 nests; females 44.4% ± 9.4%, n = 14 nests, paired t-test, t_{13} = 1.70, n.s.). Temporary egg desertion accounted for 3.76% ± 4.57% of this period (range 1-4 d, n = 14 nests). There was also no significant difference between the length of incubation shifts of males and females (average per bird, based only on complete periods; males: 5.4 ± 2.4 days, n = 14; females: 4.8 ± 2.1 days, n = 14; paired t-test t_{13} = 1.33, n.s.) and together these

averaged 5.1 days (± 2.2 days, n = 28 birds). However, the distribution was clearly bimodal, and tended to include a high number of 1-day shifts but also some 9-day shifts (Fig. 3). On 5.4% of nest-nights, the mate visited the nest, but did not exchange with the partner in incubation.

In the chick-rearing period, males visited the nests more frequently than females (males: 0.804 ± 0.104 night^{-1}, n = 16; females: 0.722 ± 0.116 night^{-1}, n = 16, paired t-test, t_{15} = 2.7, $P < 0.02$), and both sexes achieved their highest average attendance levels. The frequency of visits decreased significantly throughout this period (males: Pearson r = -0.35, n = 52 days, $P < 0.02$; females: Pearson r = -0.51, n = 52 days, $P < 0.005$), resulting in an increase in the number of nights with no visits from any parent from the first half of the period to the second half (7 out of 390 chick-nights in the first 26 days *v* 17 out of 309 chick-nights in the remaining 26 days, $\chi^2_1 = 5.61$, $P < 0.02$).

Seasonal patterns of activity

Figure 4 shows an index of activity of birds at monitored nests during the study period. We defined the index of activity (hereafter designated as activity) as the average number of complete movements (entrance plus exit) performed by birds attending their nests. There were no differences in the average levels of activity between males and females (Table 2), but there were significant differences between the three periods (repeated-measures ANOVA on averages per individual, with sex as factor; Sex: $F_{1,22} = 2.35$, n.s.; Period: $F_{2,44} = 4.26$, $P < 0.02$ - Table 2). There was no significant interaction effect ($F_{2,44}$ = 2.69, n.s.). A posteriori tests showed that birds were significantly less active during the chick-rearing period, in relation to pre-laying and incubation periods (Table 2).

There was a significant correlation between daily values of activity and attendance in the pre-laying period (Spearman r = 0.50, n = 26 days, $P < 0.01$) but not in the incubation and chick-rearing periods (Spearman r = 0.15, n = 47 days, n.s.; Spearman r = 0.21, n = 52 days, n.s., respectively).

Activity during the night and the effect of moonlight

Figure 5 shows the activity of Cory's Shearwaters at nests during the night. Within each period, we grouped the number of movements per active bird into 30 min intervals, and so the area below each line equals the average activity level for the corresponding period. Birds were generally more active at the beginning of the night, shortly after arrival. The activity decreased 1-2 h after this peak, and increased again shortly before dawn, when birds left the colony to forage at sea.

In order to assess the effect of moonlight, we compared levels of activity, hour of arrival at nests (local time) and amount of time spent inside the nests during periods of full- and new-moon. We only included data from 4 days before and after new-moon (8 days "window") and we used averages of individual birds over these periods in the analysis. Furthermore, during the full-moon periods, we only considered the days when the moon was visible at dusk (moonrise earlier than 1-h after sunset and moonset later than 4-h after sunset), when the effect was most likely to be detected (Table 3). We did not possess data on cloud coverage so this effect was not accounted for. Due to the high number of tests addressing the same underlying hypothesis, we used the sequential Bonferroni technique (Rice 1989) to determine the level of significance for the statistical tests. None of the variables tested indicated a relationship with ambient light (all paired t-tests not significant, Table 3).

DISCUSSION

The logging system

Our logging system represents a method with potential application whenever non-intrusive assessment of activity of burrow-occupying animals is desired. In fact, the simplicity of the system facilitates simple adjustments to fit particular features of each study or species. The diameter of the tubes (which can be made from any appropriate material) can be increased or decreased as long as the number of turns of the coils

and/or the magnet strength are adjusted accordingly. For smaller birds, the size and weight of the magnets can also be substantially decreased by using magnets made of rare earths, which provide strong magnetic field at very small sizes. This flexibility enables the application of the system on a wide range of studies when the access of study animals to a given area is made by a restricted/restrictable passage.

The data collected proved to be accurate, with very few missing complete movements and virtually no birds visiting the nest undetected. Identification of the sex of marked birds from magnet orientation was also exact. The reliability of the system will depend on the probability of missing some movements performed by birds, but also on the quality of the signal produced, in terms of correctly assigning the corresponding coding to entrances and exits by males and females. The likelihood of missing movements depends mainly on the total activity of the birds involved and will be greater with increasing number of monitored individuals on a single scanner and data logger and with the frequency and synchrony of their visits. High missing rates can only be decreased by reducing the number of monitored burrows per scanner. On the other hand, the quality of the signals is only influenced by the behaviour of birds inside the tubes. Very slow and very fast movements can produce distorted or incomplete coding, although generally these can still be interpreted. In such cases, facilitating or deterring devices (*e.g.* physical barriers inside the tubes) should be installed on the detection units to regulate the speed of entrance/exit in order to ensure the production of a clear coding.

Major limitations of this system include the inability to identify each bird individually. We have no records of breeding adults entering another breeding burrow, but visits by prospecting birds do occur. If prospecting birds were equipped with magnets, these could not be separated from those of the occupying pair. This limitation is potentially more serious before laying, when prospecting reaches its maximum, after which visits by alien birds are generally limited by the owners' presence (incubating or feeding their chick). Another potential source of error is that the correct assignment of movements to each sex implies that birds must enter and leave the nests always in the same way (head or tail first) so that the polarity-specific coding can be correctly interpreted. This is not a

problem for most burrow and crevice nesting birds, which tend to enter and leave head-first, preventing damage to their feathers.

Attendance, activity and effects of ambient light

As with other Procellariiformes (*e.g.* Harris 1966, Imber 1976, MacDonald 1977, Brooke 1990, Hatch 1990) the pre-laying exodus involved mainly females and in our study it lasted for c. 20 days. In contrast, 90-100% of the males visited their nest between 1 and 15 May and presented high activity levels (Fig. 2). This behaviour probably prevents burrows from being occupied by prospecting birds or by established neighbouring pairs, and can also guard against extra-pair copulations (Hatch 1987, Birkhead & Moller 1992). The fact that attendance and activity levels were correlated during this period suggests the possible existence of agonistic interactions, supporting a nest- or mate-guarding hypothesis.

During the incubation period, mates spent similar amounts of time incubating and performed similar incubation shifts. These observations contrast with those of Mougin *et al.* (1988) at Selvagem Grande, who found that males tended to undertake longer incubation shifts than females. The values in this study (average of 5.4 days) compare with 8.5 days in the Aegean Sea (Ristow & Wink 1980) and 8.4 days in the Selvagem Grande over seven years (Mougin *et al.* 1988) and suggest that birds on Berlenga Island feed relatively close to the colony. This is further supported by the observation of occasional visits to the nest by a member of a pair without the occurrence of a changeover.

After the chick had hatched males attended the colony more often than females. Similar patterns of attendance by the sexes were observed in the Wandering Albatross *Diomedea exulans* (Tickell 1968) and Fulmar (Hatch 1990). In the former species, males fed their chick slightly more often than females. Whether the differences observed in Cory's Shearwaters reflect disparities between levels of food provisioning by each sex is unclear.

During chick-rearing, birds visited the nest frequently, possibly to ensure regular provision of food. Throughout this period, attendance levels decreased slightly but significantly as growth progressed and, as expected, this resulted in an increase in the proportion of chicks receiving no visits from their parents. During the study, an average of 96.5% of the chicks were visited by at least one parent each night. Comparable data on the same subspecies include those of Klomp & Furness (1992) in the Azores (56% nests visited per night) and Hamer & Hill (1993) on Selvagem Grande (79% of the chicks fed by at least one adult). Round & Swann (1977) reported an average of about 80% of nests attended in the Mediterranean race *C.diomedea diomedea*. The visitation levels on Berlenga island are among the highest reported for nocturnal Procellariiformes (Warham 1990, Klomp & Furness 1992 and references therein) and suggest that other studies may have underestimated attendance levels, by missing brief or late visits by study birds or visits in which chicks were not fed. Otherwise it may indicate that birds feed close to the colony, possibly within the waters of the Portuguese continental shelf.

The levels of activity were relatively variable during the pre-laying and incubation periods. There was a general decrease in the activity towards the start of laying, followed by an irregular pattern through most of the incubation period. After hatching, the patterns of activity changed dramatically: the number of movements suddenly stabilised around 1.5 movements per bird, with very little variation between days and individuals. The timing in the peaks of activity varied across the breeding season. These observations suggest that birds adjusted their behaviour to variation in the period of darkness, and so to the hours of sunrise and sunset, as observed in other species (Warham 1990 and references therein).

Moonlight avoidance has been reported in several Procellariiform species, with smaller species generally showing higher sensitivity to levels of ambient light (*e.g.* Harris 1966, Boersma *et al.* 1980, Watanuki 1986, Warham 1990, Brooke & Prince 1991, McNeil *et al.* 1993). These observations have been interpreted as a response to increased risks of predation and/or disturbance at their breeding grounds, along with generally ineffective

defence mechanisms. Indeed, many petrels are heavily exploited by gulls and skuas at their colonies (*e.g.* Watanuki 1986, Furness 1987). However, some species maintain nocturnal attendance even in the absence of predation (McNeil *et al.* 1993) and at the Galapagos Islands two similar-sized storm-petrels occur one being diurnal and the other nocturnal (Harris 1969). These observations suggest that predation is possibly not a universal explanation for this behaviour.

Despite their size, Cory's Shearwaters are strictly nocturnal at their breeding grounds, except on the Selvagem Grande where they come ashore a few hours before sunset (Zino 1971). There are no marked differences in the abundance of predators or levels of human disturbance within the Atlantic colonies, so that the predator avoidance hypothesis seems to be insufficient to account for such differences in behaviour. Klomp & Furness (1992) suggested that Cory's Shearwaters in the Azores responded to levels of ambient light, decreasing their nest attendance and arriving later on moonlit nights. By comparing their observations with the daylight attendance of birds at Selvagem Grande, they suggested that the response could be related to prey availability rather than being an anti-predator strategy.

Jouanin *et al.* (1989) and Bretagnolle (1990) failed to find any effects of moonlight on incubating Cory's Shearwaters on Selvagem Grande and our study provides further evidence of this lack of sensitivity among breeding birds throughout the breeding season. Moonlight influences non-breeding birds in terms of overall attendance and particularly affects their aerial and vocal activity (Storey & Grimmer 1986, Bretagnolle 1990), but produces little effect on birds rearing chicks (Warham 1990, Hamer & Hill 1993). In view of the diversity in patterns of attendance and in sensitivity to moonlight within the same species and region, it is likely that several factors act simultaneously. Apart from predation, possible key-factors include prey behaviour and availability, habitat structure (strongly structured habitat with many obstacles will discourage nocturnal behaviour) and colony density (high competition for nest sites will favour early arrival at the colonies).

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Table 1. Reliability analysis for the logging system on Cory's Shearwater (N = total number of complete movements performed by birds - see text for details on computations)

Period	Paired movements (entrances and exits recorded) $N*(1-q)^2$	Unpaired movements (one entr. or one exit not recorded) $N*2q(1-q)$	Probab.missing a single movement q	Estimated missing two single movements $N*q^2$	Average [± SD (N)] number of complete mov. ($bird^{-1}.d^{-1}$)	Estimated missing presences $N*[(q^2)^{avg.mov}]$
Pre-laying (26 days)	496	19	0.019	0.2	2.18 ± 1.62 (24)	1.88×10^{-5}
Incubation (47 days)	1571	85	0.026	1.1	2.10 ± 0.84 (30)	3.65×10^{-4}
Chick-rearing (52 days)	1674	162	0.046	3.9	1.50 ± 0.37 (32)	0.18
Total (125 days)	3741	266	0.034	4.7	1.75 ± 0.49 (32)	0.03

Table 2. Activity (number of complete movements per bird visiting the nest) in relation to sex and phase of the breeding season (see explanation in text).

	Pre-laying	Incubation	Chick-rearing
Males	2.73 ± 1.87 n=12	2.22 ± 0.75 n=15	1.53 ± 0.35 n=16
Females	1.63 ± 1.16 n=12	1.98 ± 0.93 n=15	1.47 ± 0.39 n=16
TOTAL	2.18 ± 1.62 n=24	2.10 ± 0.84 n=30	1.50 ± 0.37 n=32

Table 3. Levels of activity, time of arrival at the nest and amount of time spent by Cory's Shearwaters inside the burrows in relation to phase of the moon during the breeding season

		Pre-laying	Incubation	Chick-rearing
Activity (movements per bird)	No moon	2.09 ± 0.44	2.27 ± 1.09	1.49 ± 0.47
	Full moon	2.34 ± 0.80	2.33 ± 2.77	1.47 ± 0.46
	Paired t-test	t=1.19, 7 df n.s.	t=0.10, 24 df n.s.	t=0.17, 31 df n.s.
Hour of arrival	No moon	22.05 ± 00.13	23.49 ± 01.25	23.36 ± 01.38
	Full moon	22.43 ± 00.52	00.50 ± 02.16	23.55 ± 01.24
	Paired t-test	t=1.78, 6 df n.s.	t=1.559, 16 df n.s.	t=1.00, 31 df n.s.
Time inside the burrows (h)	No moon	02.32 ± 00.35	01.22 ± 01.17	02.24 ± 01.30
	Full moon	01.48 ± 00.43	01.06 ± 01.08	02.28 ± 01.22
	Paired t-test	t=2.26, 7 df n.s.	t=0.80, 22 df n.s.	t=0.24, 31 df n.s.

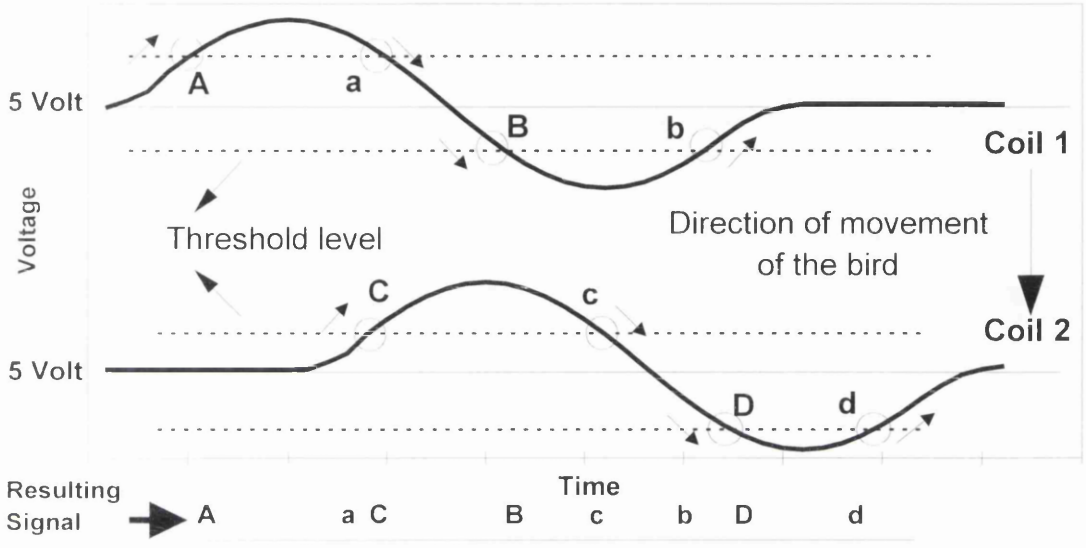

Figure 1. Changes in voltage induced on the detection unit by the passage of a magnet, and corresponding coding of the events (bottom of the scheme - see text for explanations).

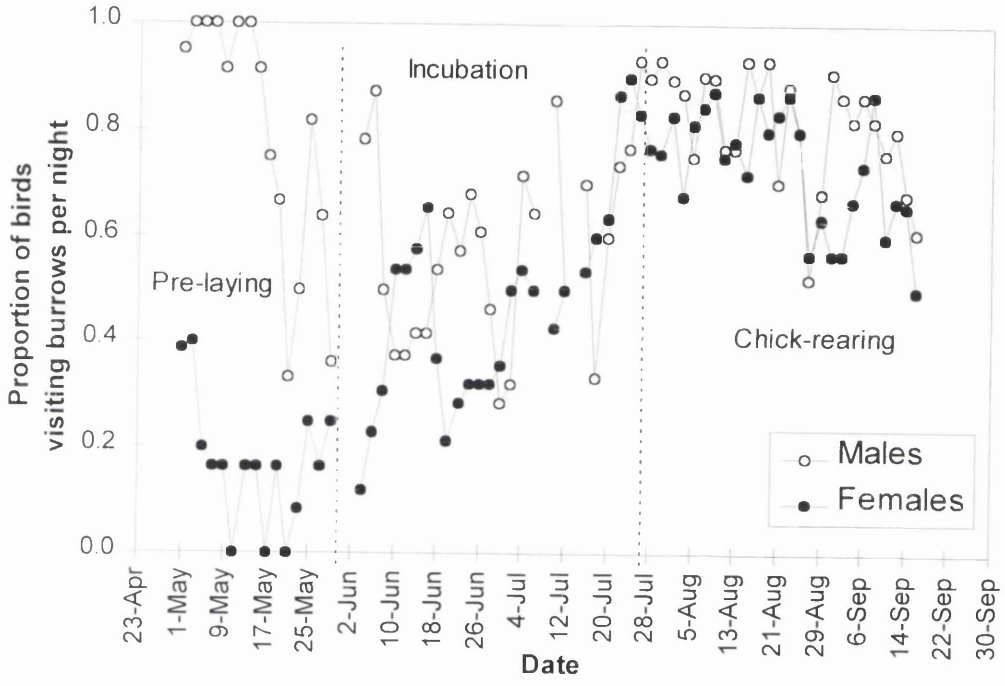

Figure 2. Attendance of male and female Cory's Shearwaters during the breeding season (data grouped for 2-d periods). Interrupted data lines represent periods of system failure.

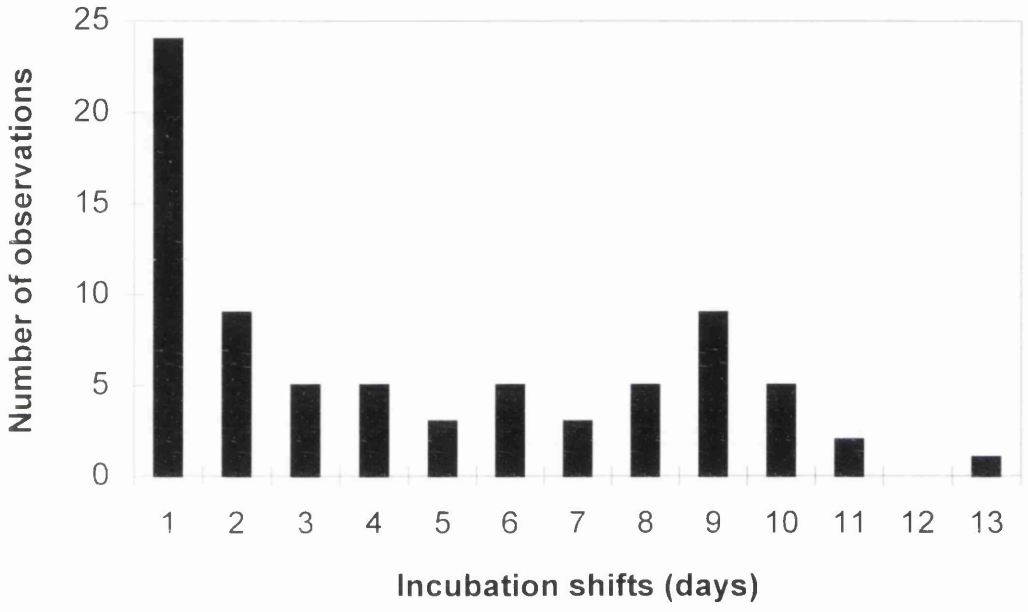

Figure 3. Incubation shifts of Cory's Shearwater ,1 June - 15 July (for explanation, see text).

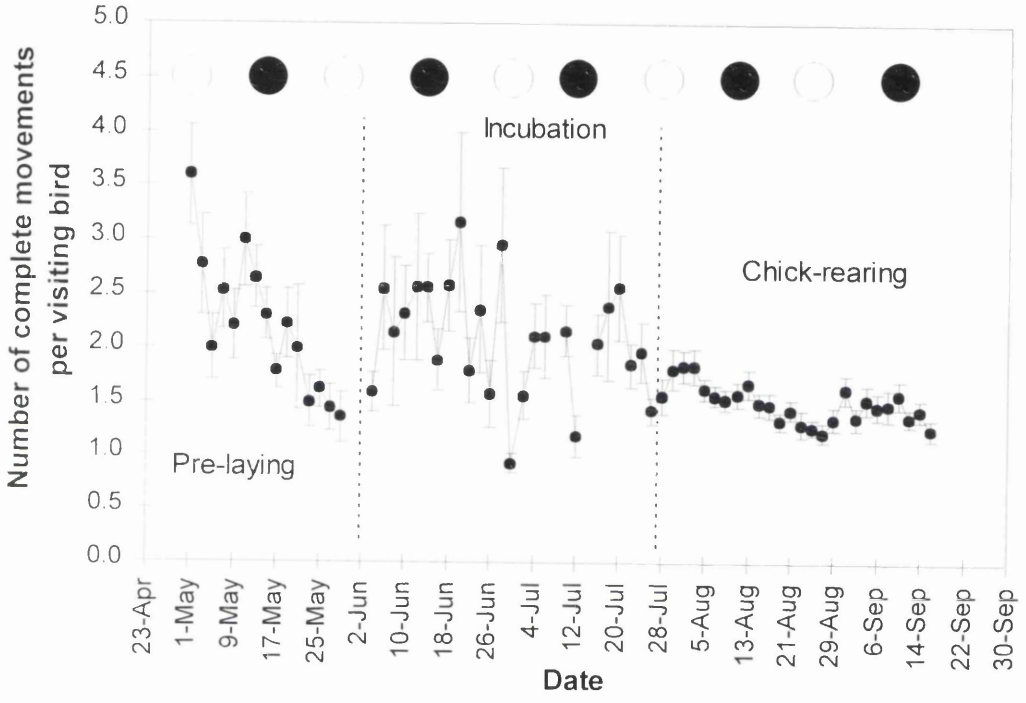

Figure 4. Levels of activity of Cory's Shearwater during three stages of the breeding season (data grouped for 2-d periods). Full-moon (open circles) and new-moon (filled circles) periods are shown. Interrupted data lines represent periods of system failure. Points represent means ± standard error.

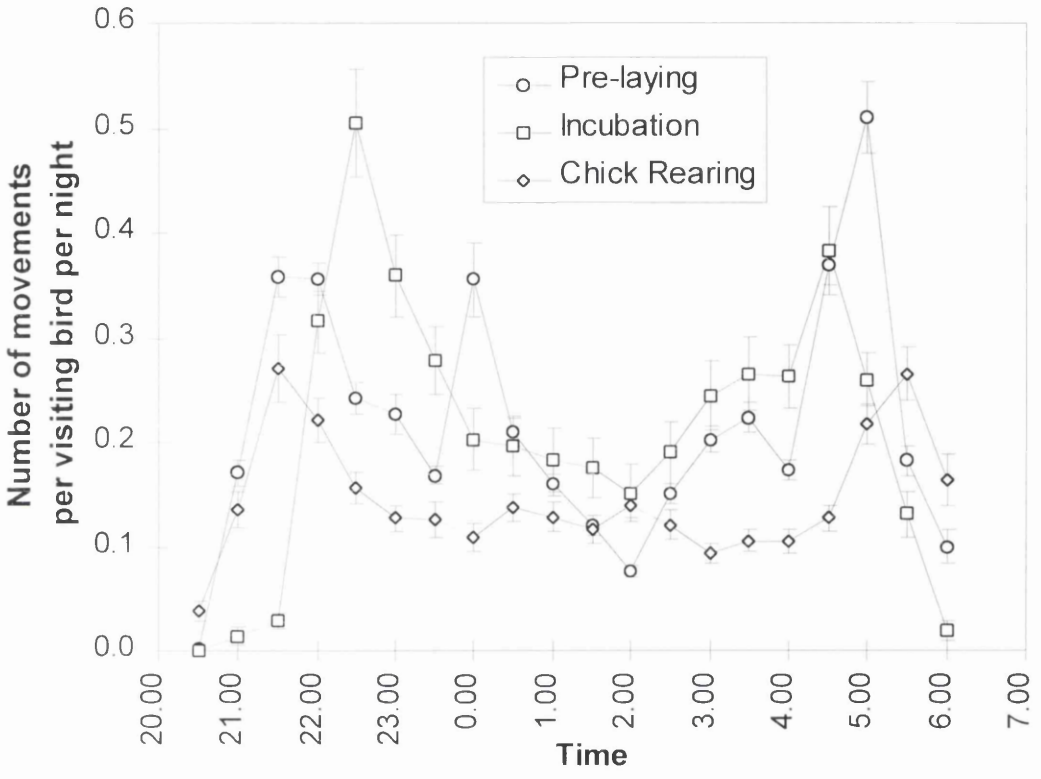

Figure 5. Levels of nocturnal activity of Cory's Shearwater during the three stages of the breeding season. Points represent means ± standard error.

Chapter 7

Flexible foraging strategy of Cory's shearwater *Calonectris diomedea* during the chick rearing period

In Press as:

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Abstract. Procellariiformes are renowned for exhibiting low rates of food provisioning to their slow growing chicks. In some species, the patterns of food delivery to chicks have been deduced from changes in their weight, obtained from periodic weighings. However, the behaviour of individual parents can not be resolved using this method. In this study, a periodic weighing protocol was applied to Cory's shearwater Calonectris diomedea chicks at Selvagem Grande, north east Atlantic. This information was complemented by examining the attendance of individual parents, using an automatic logging system. During this study, chicks were fed infrequently, and were in significantly poorer condition when compared with other years and other colonies. This suggests that adults were experiencing some difficulties in finding an adequate food supply close to the colony. Under these conditions, individual parents adopted a dual provisioning strategy, switching between short and long foraging trips, a previously undescribed behaviour in any northern hemisphere petrel species. Although the average meal size following long trips was higher than that after short trips, the average amount of food provisioned per day spent at sea decreased, and so chicks did not benefit from longer trips. This finding suggests that long trips can be used to restore adult body condition, presumably depleted during short trips as shown previously for some petrels and albatrosses. The adoption of this flexible foraging strategy, which differs from the uniform intervals observed in Cory's shearwaters experiencing situations of 'normal' food abundance, may represent a mechanism through which breeding birds compromise between the needs of their chicks and the maintenance of their own body condition.

Extreme life-history traits of Procellariiform seabirds have long been viewed as reflecting constraints arising from spatial and temporal unpredictability of food resources in the marine environment and by limitations imposed by the costs of transporting food from presumed distant foraging areas (Lack 1968; Ashmole 1971; Ricklefs 1983). Single clutch size, and the development pattern of chicks, particularly the prolonged fledging period resulting from slow growth, and the large accumulation of fat, are among the most quoted adaptations to such an unpredictable environment (Boersma et al., 1980; Ricklefs et al. 1985; Boersma & Parrish, in press).

Life-history theory predicts that in long-lived species, such as Procellariiformes, the investment in a given breeding episode should be adjusted in relation to prospects of parental survival and future reproductive investments (Stearns 1992). In this context, an extensive body of literature has addressed the mechanisms through which the provisioning of food to chicks is regulated. Lack (1968) suggested that breeding birds would experience occasional periods of unfavourable oceanographic conditions and low food availability, which would prevent them from returning regularly and frequently to feed their chick. The resulting low provisioning rates would sustain slow chick growth (Ricklefs 1983). Large accumulations of fat by chicks during the nestling period were interpreted as representing a selective benefit, by providing an insurance against prolonged intervals between feeds, resulting from periods of food shortage. More recently, Ricklefs & Schew (1994) demonstrated that the natural patterns of food delivery could be replicated by assuming that individual birds maximize the rate at which food is acquired, and that this rate exhibits stochastic variability. Individuals were further supposed to base their decision to return to feed their chick on the state of their own condition (Ricklefs & Schew 1994). Under these assumptions, birds are expected to provide more than the food needed to fulfil current chick demands, to avoid exposing them to prolonged periods of starvation, likely to increase the risk of mortality. Such periods would occur because of stochastic variation in individual foraging success, in addition to any variation in feeding opportunities to all birds in a colony. This explanation views fat deposits as resulting from this 'chronic' overfeeding and predicts that Procellariiformes should have only limited ability to respond to short-term requirements of chicks. Whilst most studies

have supported the latter hypothesis, which proposes an almost exclusively parental-controlled regulation of food delivery, there is none the less some contradictory evidence. Recently, several authors demonstrated that to some extent adult birds do have the ability to respond to short-term requirements of the chicks (Bolton 1995a,b; Weimerskirch et al. 1995, 1997a; Hamer & Thompson 1997), suggesting that slow chick development and fat accumulation may result from selective pressures other than resource availability to adults (Bolton 1995a, b).

Most studies have addressed the question from the point of view of the chick (Schaffner 1990 a,b), and have included examination of the pattern and variability in food delivered at the nest (in terms of amount of food provisioned and corresponding frequencies) in natural conditions (Ricklefs et al. 1985; Hamer & Hill 1993, 1997; Bolton 1995a; Hamer et al. 1997) or in situations when chick demands or adult foraging performance were experimentally manipulated (Ricklefs 1987, 1992; Hamer & Hill 1994; Bolton 1995b; Mauck & Grubb 1995; Weimerskirch et al. 1995, 1997a). However, Chaurand & Weimerskirch (1994) and Weimerskirch et al. (1994) showed that considerable insight into the foraging patterns of Procellariiformes could be achieved by focusing on the individual parents, rather than on pair provisioning rate, or on the chick. They were able to describe a particular foraging strategy by which some albatrosses and petrel species adopted short and long trips, and established a causal link with adult body condition, in line with the parental-controlled mechanism proposed by Ricklefs & Schew (1994). However, the existence of such a behavioural mechanism regulating individual foraging decisions cannot be resolved by examining what happens to the chick at the nest.

That particular foraging strategy, which involves switching between alternative short or long foraging trips, implies an average low feeding periodicity. Such a behaviour has never been documented in shearwaters, nor in any Procellariiform species in the northern hemisphere. Indeed, in the north east Atlantic, several studies have reported relatively high rates of food provisioning to petrel chicks, ranging from 0.7 meals.chick^{-1}.day^{-1}, in Cory's shearwater Calonectris diomedea (Klomp & Furness 1992) to 1.6 meals.chick^{-1}.day^{-1} in little shearwater

Puffinus assimilis (Hamer 1994), with a maximum of 4.6 meals.chick^{-1}.day^{-1}, in the fulmar (Hamer & Thompson 1997; Hamer et al. 1997)

This raises the question of whether the these alternative foraging trips, which would only be triggered below a given threshold of chick or adult body condition, would occur amongst north Atlantic Procellariifomes, for which high rates of chick provisioning (implying abundant food supply) appear to be the norm.

Cory's shearwater breeds in the sub-tropical north east Atlantic and in the Mediterranean, with the main colonies of the Atlantic subspecies C. diomedea borealis concentrated in the Azores, Madeira and Canary islands (Martin et al. 1991; Zino & Biscoito 1994; Monteiro et al. 1996). The pattern of food provisioning in this species has been examined at Selvagem Grande (Hamer & Hill 1993), an oceanic island lying about 300 km south of Madeira archipelago, and indicated that birds are able to deliver food at a relatively high rate (0.7-0.9 meals.chick^{-1}.day^{-1}, Klomp & Furness 1992, Hamer & Hill 1993, Mougin et al. 1997b, J.P.Granadeiro, unpublished data). None the less, the surrounding waters exhibit low productivity (Ashmole 1971) and hence occasional periods of low food availability are likely to occur. Because there are no data on the abundance or availability of food in different years in the foraging area of these birds, we made the assumption that high rates of chick provisioning reflect high food availability and low rates reflect low food availability (e.g. Monaghan et al. 1994; Hamer et al. 1997; Weimerskirch et al. 1997a). In this paper, we describe the provisioning strategy of Cory's shearwater at the Selvagem island in a period of presumed low food availability. We focus on the behaviour of individual parents, by using an automatic logging system which enables monitoring the movements of each adult at the nest and we compare the results with data obtained in situations of apparent better feeding conditions, both in the same and at other locations.

METHODS

We conducted fieldwork between 12 August and 4 September 1997 on Selvagem Grande island (30°09'N, 15°52'W, hereafter referred to as Selvagem), about 300 km

south of Madeira. The breeding population of Cory's shearwater on Selvagem is currently estimated at about 13000 pairs (Mougin et al. 1996a). In this species, hatching is relatively synchronized, occurring between mid July to the first week of August (Granadeiro 1991). On 12 August, we randomly selected 32 burrows of Cory's shearwater (chicks aged 16-36 days) and equipped each with an activity logger, designed to monitor attendance at the nest. The logging equipment stores information concerning timing, direction and identity (male or female of a pair) of birds moving into and out of the nests, which can subsequently be downloaded to a computer for analysis (see Granadeiro et al. (in press) for a full description of the system). The correct operation of the system requires that study birds are previously equipped with a polarity-specific oriented magnet, and enter the burrow through a coil, which constitutes the detection unit (Granadeiro et al., in press).

Birds were captured by hand under license, ringed and sexed from vocal characteristics (Bretagnolle & Lequette 1990) or using a discriminant function based on bill measurements (Granadeiro 1993). A cylindrical magnet (30 mm long, 3 mm diameter, weighing less than 1 g), was glued to the base of a tail feather, using cloth-backed tape. The polarity of the magnet determines the type of signal produced in the coils and this enables the distinction between mates at each nest (Granadeiro et al. in press). All males received magnets with the same polarity, opposite to that of females. Before being released, we marked birds of a pair with different colours in the forehead feathers, to enable validation of information provided by the loggers by field observations at the nests. On some occasions there was a high number of birds prospecting nests in the study area, and to avoid fitting non-breeding adults with magnets, most birds were only marked if feeding evidence was obtained (e.g. chick begging interspersed with silent periods, remains of stomach oil in the bill or feathers). The logging system was first connected on 14 August, to confirm correct operation and assess reliability of the system.

To determine the amount of food delivered by adults, we weighed chicks in study nests, at 6-h intervals (with an electronic balance, to the nearest 1 g), starting at 1900 hours, from 22 to 29 August, following the protocol proposed by Ricklefs (1984) and Ricklefs et al. (1985). Each weighing took about 1 hour to complete and

chicks were always weighed in the same order. None of the chicks regurgitated any considerable amount of food while handling. Meal size was estimated as the sum of positive weight increments recorded between weighings (hereafter referred to as SUM, following Ricklefs (1984)). Values of SUM underestimate the size of meals, because they do not account for losses due to respiration and excretion (Ricklefs 1984; Ricklefs et al. 1985). Correction procedures involve either adding a fixed amount, assuming constant average rates of weight loss (Ricklefs et al. 1985; Klomp & Furness 1992; Hamer & Hill 1993) or correcting each SUM from calculated relationships between these rates and chick age, initial mass and meal size (Bolton 1995a; Lorentsen 1996; Hamer & Thompson 1997). None the less, many authors present information concerning uncorrected values of SUM, and these values are adequate for the comparative approach in this study. We excluded from computations of meal sizes all situations when two adults visited the nest during the night, since generally the weight increments could not be associated with an individual parent.

On 19 August, we weighed and measured wing length (maximum flattened chord, to the nearest mm) of study chicks at 1900 hours, and 20 August at 0800 hours. This procedure was also applied to a group of 30 chicks, in the vicinity of the study area, which acted as control for effects of the logging equipment on feeding frequency.

Comparative data were obtained at Selvagem and Berlenga island (39°24'N, 9°30'W, off the Portuguese mainland) on several occasions, during the course of other studies (Granadeiro 1991; Granadeiro et al. in press: J.P.Granadeiro, unpublished data). Thus, wing measurements and weight of chicks were obtained in Selvagem in 1993 (on 22 August), and Berlenga island in 1987 (19 August), 1995 (2 August) and 1996 (12 August).

Rates of wing growth are relatively insensitive to short-term variation in food supply (Ricklefs et al. 1980; Ricklefs 1992; Mauck & Grubb 1995). There were no significant differences between colonies and years in the slopes of weight-wing length relationships (ANCOVA: for differences of slope, $F_{4, 161} = 1.5$, NS). Therefore, in order to calculate an index of body condition, we pooled data from both colonies in these years and modelled the relationship as:

Weight (g) = 10.22(SE=0.43)*Wing length (mm) - 124.02(SE=29.08),

$r^2 = 0.77$, $F_{1, 169} = 569.3$, $P < 0.0001$

Body condition was calculated from the residuals, expressed as a proportion of the predicted value, following Hamer & Hill (1993) and Bolton (1995a). Control chicks were further weighed at dusk and dawn on 24 and 28 August, to assess effects of equipment and periodic weighing throughout the night.

Duration of adult foraging intervals was determined as the period between successive records of a given adult between 22 and 29 August, hereafter referred to as study period. To avoid under-representing long intervals, we considered all feeding intervals starting in this period, even if they extended beyond 29 August (but before 4 September, when we left the island)..

Prior to the application of statistical tests, we checked data for normality and homogeneity of variances, and used non-parametric tests if one of these conditions failed to be met, following Zar (1996). Some of the data analysed in this paper represent repeated measurements on the same individuals, and in these cases we calculated test statistics on means per individual bird, to avoid potential problems arising owing to pseudoreplication (Hurlbert 1984; Leger & Didrichsons 1994). Throughout this paper, we present means ± standard deviation.

RESULTS

Effects of equipment and periodic weighing protocol

Although there was an effect of date on chick weight, related to growth, there were no significant differences between weight of study and control chicks during the study period and both groups gained weight at similar rates (Table I, repeated-measures ANOVA on chick weight on 19, 24 and 28 August: effect of date, $F_{2, 120} = 70.8$, $P<0.001$; between-groups effect, $F_{1,60} = 0.13$, NS; interaction effect, $F_{2,120} = 0.98$, NS). There were also no significant differences between control and study nests

in the amount of food delivered by adults, estimated as the average positive weight variation from dawn to dusk (Table I, two-way ANOVA: effect of date, $F_{2,90} = 0.44$, NS; between-group effects, $F_{1,90} = 0.91$, NS; interaction effect, $F_{2,90} = 0.01$, NS). Furthermore, in none of the control dates did we detect significant differences between the proportion of chicks fed at control and study nests (Yates corrected chi-square tests: $\chi_1^2 = 0.24$, $\chi_1^2 = 0.00$, $\chi_1^2 = 0.06$, on 19, 24 and 28 August, respectively, all NS).

Chick body condition

There were significant differences in average body condition between colonies and years (Table II, one-way ANOVA: $F_{4,166} = 17.1$, $P<0.0001$). Post hoc comparisons (Student-Newman-Keuls) revealed the existence of three significantly different groups (Table II): Berlenga (1987), which presented the highest condition scores; Selvagem (1997), with the lowest values; and the three other colonies (years), with indistinguishable intermediate values. The idea that chicks in 1997 were in comparatively poorer condition is further supported by the significant differences between the mean weight of study chicks and those obtained by Klomp & Furness (1992) in the Azores and Hamer & Hill (1994) in Selvagem, at approximately the same time of year (24 August 1989: 770 ± 91 g, $N=15$ (Klomp & Furness 1992); 19 August 1993: 673.8 ± 87.2 g, $N=30$ (Hamer & Hill 1994); 22 August 1997: 519.9 ± 122.6 g, $N=32$ (this study); one-way ANOVA, $F_{2,74}=35.5$, $P<0.001$). Post hoc tests revealed that significant differences were only obtained in pair-wise comparisons involving Selvagem in 1997 (all other comparisons were not significant).

Feeding frequency and intervals between meals

In 1997, chicks were fed infrequently compared with other years and colonies (Table III). There were significant differences in the estimated feeding frequency among colony in different years (Table III, one-way ANOVA, $F_{3,65}=21.39$,

P<0.0001), but significant differences were only found in pair-wise comparisons involving Selvagem in 1997 (Student-Newman-Keuls post hoc tests).

Intervals between meals delivered to chicks ranged from 1 to 6 days (Fig. 1), with an average (per nest) of 1.9±1.1 days (N=32 nests). This value differed significantly from the values obtained on Berlenga, in the same period in 1996 (1.1 ± 0.2 days, N=10 nests, Mann-Whitney U-test: U=74, P=0.01, Fig. 1). In Selvagem, in 1991, the average interval between feedings was 1.3 days and the maximum number of days chicks experienced without feeding was 4 days (Hamer & Hill 1993). This occurred on 0.8% of the intervals reported (N=261 intervals), much less frequently than in our study (16.3%, N=98 intervals, Fisher's exact test: P<0.0001).

Duration of individual foraging trips and amount of food delivered

Males and females did not differ in frequency of visits to the nest (males: 32.6%, females: 29.5%, N=448 parent.nights, Yates-corrected chi-square test: χ_1^2 = 0.38, NS) or in the corresponding feeding intervals (males: 3.3±2.3 days, N=59; females: 3.0±2.0, N=56, Mann-Whitney U-test: U=1512.5, NS). The distribution of these intervals was bimodal in males and females, in sharp contrast with observations in Berlenga (1996), where individual adult attendance was also monitored (Fig. 2). Despite an apparent disparity in the occurrence of 2-day intervals in each sex, there were no significant differences in distribution between the sexes (Kolmogorov-Smirnov two-sample test, maximum absolute difference = 0.10, NS).

Birds did not alternate short (1 to 2 days) and long (3 to 9 days) intervals. Of 58 consecutive trips, 55.2% corresponded to alternate trips while 44.8% involved succession of the same type of trip, so they were adopting either type trips at random (chi-square: χ_1^2 = 0.14, NS).. Males and females adopted short and long trips in similar proportions (Yates-corrected chi-square: χ_1^2 = 0.23, NS) and birds spent about 20.4% of their time in short trips and 79.6% in long-trips (N=448 parent.nights). Birds started short and long trips irrespective of date (Spearman rank correlation: r_s = 0.11, N=7, NS).

Males and females did not differ in the amount of food delivered to chicks in either short and long trips (short trips: t test, t_{22}=2.0, NS; long trips: t test, t_{34}=0.7, NS), so data from both sexes were pooled. Meals delivered after long intervals were almost twice as those provided after short trips (short trips: 56.6 ± 38.0 g, N=33; long trips: 125.0 ± 36.5 g, N=60, t test t_{71}=7.8, P<0.0001). However, the increase in meal size did not compensate for the greater interval between feeds associated with long trips, i.e. the ratio between meal size and foraging interval decreased with increasing trip duration, such that short trips resulted in a greater rate of food delivery to the nest (Fig. 3). On seven occasions (N=116 foraging trips), birds visited the nest but no increase in chick weight was observed (therefore not included in the previous analysis). All these situations followed short trips.

The meal size after a short trip did not differ significantly from the estimated mass delivered by a single adult on Selvagem in 1991 (mean=59.0 ± 22.4 g, N=236 (Hamer & Hill 1993); t test, t_{283} = 0.87, NS). Similarly, the average nightly food delivery (zero meals included) recorded in 1997 did not differ from values obtained in other colonies (Table IV, one-way ANOVA $F_{3,756}$ = 0.59, NS), but presented a considerably higher variability.

DISCUSSION

We did not detect any evidence of deleterious effects of the equipment or of the weighing protocol on the provisioning behaviour of Cory's shearwater. Although some birds stopped at the entrance of the nest on the night following the installation of the logging equipment, they all soon entered the nest to feed their chick. The same applies to the periodic weighing procedure. A few birds standing at the entrance of the burrows moved away as we approached to weigh chicks. However, the fact that study chicks grew at the same rate as control birds and were fed with equal frequencies suggests that these parents returned later in the night and resumed feeding. These findings conform with previous observations that indicated a lack of detrimental effects of manipulation during chick rearing periods in many

Procellariiformes (Hamer & Hill 1993; Bolton 1995a; Hamer & Hill 1997; Hamer & Thompson 1997).

Cory's shearwater chicks do not usually experience prolonged periods without feeding, as a result of relatively high average feeding frequencies (Hamer & Hill 1993, 1994; Mougin et al. 1996b; Granadeiro et al., in press; Table III). In contrast, chicks at Selvagem in 1997 were infrequently fed, and presented one of the highest mean feeding intervals reported for Procellariiformes in the north-east Atlantic (Hamer & Hill 1993; Bolton 1995a; Hamer & Thompson 1997). Moreover, in 1997, chicks were in comparatively poorer body condition, which indicates that, at some stage, adults were not able to ensure them an adequate provision of food. These observations suggest that parents were having difficulties in gathering enough food close to the colony, and were forced to undertake longer foraging shifts.

Under these circumstances, individual birds were adopting an alternative provisioning strategy, consisting of short and long visiting intervals, previously undescribed in this species, but apparently similar to that exhibited by some albatrosses and petrels in the southern oceans (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994, 1997a, b). In our study, birds spent most of their time in long trips, during which they were able to deliver almost twice as much food as in short trips. Differences between food loads in short and long foraging trips were also recorded in some small petrel species (blue petrel Halobaena caerulea and thin-billed prion Pachyptila belcheri) but by contrast albatrosses deliver the same amount of food in both kinds of trip, albeit with higher energy contents in long trips (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994, 1997b).

Previous studies examining patterns of food delivery in Cory's shearwater (Klomp & Furness 1992; Hamer & Hill 1993; Mougin et al. 1996b) did not assess individual foraging behaviour, and the number (but not the identity) of adults feeding its chick in a single night was ascertained from the magnitude of chick weight increments. Consequently, direct comparison with our data is not possible, but the comparatively low maximum number of days without feeding reported in 1991 on Selvagem (4 days, 0.8% of all feeding intervals, Hamer & Hill 1993), suggests that under the prevailing (presumed 'normal') feeding conditions, birds were not

following the dual provisioning strategy described in this study. Moreover, individually monitored adults at Berlenga island in 1996 (Granadeiro et al., in press) fed their chicks very frequently (Table III) and clearly did not exhibit such foraging behaviour (Fig. 2).

The strategy of making either long or short trips has been interpreted as a means of regulating investment in offspring. In all species which present this provisioning pattern, long foraging trips were associated with an improvement in adult body condition, whereas short trips were undertaken at the expense of body reserves (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994, 1997b). Despite resulting in a decrease in adult condition, these short trips represent a benefit to chicks by ensuring a more regular food delivery, which appears to be more profitable (Schaffner 1990a) and certainly decreases the likelihood of starvation. That adult birds will not generally allow their condition to deteriorate below a minimum body condition threshold is supported by the lack of compensatory response in situations of natural or experimentally increased foraging effort or demands at the nest (Sæther et al. 1993; Mauck & Grubb 1995; Weimerskirch et al. 1995). In our study, we did not examine variation of adult body condition in relation to feeding interval, nor did we have any indication of the location of the foraging areas, which can only be efficiently assessed through satellite telemetry (Weimerskirch et al. 1994, 1997b). In fact, birds at Selvagem were already subjected to the installation of the logging equipment, followed by the capture and subsequent application of the magnets and to the periodic weighing protocol over a relatively short period and further disturbance (repeatedly weighing adults at the nest) might have induced significant changes in provisioning behaviour and perhaps disrupt breeding.

However, there are striking similarities between the behaviour of Cory's shearwater and that of other petrels undertaking short and long foraging trips in which condition was monitored, strongly suggesting that a similar regulation process is involved. Moreover, although long trips yielded comparatively larger food loads, the net food delivery (meal size per number of days spent foraging) decreased considerably after 2 days (Fig. 3), indicating that this strategy did not represent a benefit to chicks, so presumably must benefit adult body condition.

Mougin & Jouanin (1997) showed that incubating Cory's shearwater at Selvagem can forage as far away as the east coast of Africa (Morocco and Mauritania) and these productive upwelling areas also represent potential feeding zones for birds rearing chicks. These authors showed that birds could reach the African coast in about 1.5 days (31-37 hours), which would result in a feeding interval of more than 3 days, in line with our observation of long foraging trips (Fig. 1). The less profitable short trips could have resulted from foraging in the oceanic area surrounding the colony, but this remains a matter of speculation.

Despite the marked differences in the relationships between the size of meals provisioned to chicks and the frequency at which they were delivered in different years at Selvagem, there was a striking similarity in the resulting average food provisioning rates (Table IV). Although Selvagem (1997) presented the lowest and more variable nightly food delivery rate (Table IV), the differences between colonies (years) were not significant. This result suggests that deterioration of chick condition probably occurred before the start of this study, and adults were still unable to compensate for the requirements of chicks at the nests.

Our results suggest the existence of a trade-off between food load and provisioning frequency, indicating that in situations of presumed low food availability individual parents delivered comparatively larger meals but visited the nests less frequently. Chicks were exposed to considerably longer intervals between feeds, which arose from the fact that parents were undertaking a dual foraging strategy. Conversely, our results suggest that under favourable feeding conditions, birds will deliver smaller meals, at a higher frequency, and consequently reduce the variability in the provisioning rate, arising from stochastic variation in foraging success (Ricklefs & Schew 1994). The adoption of such a distinct behaviour by the same population under a different feeding context suggests that this can be a widespread mechanism in Procellariiformes to cope with occasional situations of low resource availability, and the issue clearly deserves further investigation. This strategy provides an increased flexibility to exploit a wide range of food availability scenarios, and efficiently allows adult birds to compromise between the needs of their chick and

the maintenance of an adequate level of their own body condition, as suggested by Weimerskirch et al. (1994, 1997a, b) and Chaurand & Weimerskirch (1994).

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Table 1 - Weight (in g) of control and study chicks at 1900 hours during the study period, and average mass increments (only positive weight variation were included, in g)

Date	Weight of chicks (g)		Average positive mass increments (g)	
	Control nests (N=30)	Study nests (N=32)	Control nests	Study nests
19 August	456.5 ± 131.3	464.9 ± 116.5	87.5 ± 64.3 (19)	97.3 ± 79.3 (14)
24 August	596.5 ± 142.7	546.3 ± 136.7	83.0 ± 49.6 (15)	97.6 ± 58.8 (17)
28 August	611.5 ± 142.5	592.7 ± 125.4	97.7 ± 61.5 (15)	111.4 ± 71.2 (16)

Values represent means ± standard deviation, sample size in parenthesis.

Table II - Index of body condition of chicks of Cory's shearwater obtained in Selvagem Grande and Berlenga islands (means ± standard deviation, sample size in parenthesis), dates when measurements were obtained and corresponding post-hoc tests (Student-Newman-Keuls) on pairwise comparisons of condition indexes

Colony (Year)	**Date of measurements**	**Index of body condition**	**Post-hoc tests**
Berlenga (1987)	19 August	0.14±0.08 (21)	A
Berlenga (1995)	2 August	0.03±0.13 (17)	B
Berlenga (1996)	12 August	0.04±0.23 (19)	B
Selvagem (1993)	22 August	0.05±0.15 (52)	B
Selvagem (1997)	19 August	-0.12±0.14 (62)	C

Different letters indicate colonies (years) that differ at $P<0.05$.

Table III - Feeding frequencies (proportion of nights when food received, calculated as average per nest) of Cory's shearwater obtained in Berlenga and Selvagem islands, and corresponding post-hoc tests (Student-Newman-Keuls)

Colony (Year)	Feeding frequency	Post-hoc tests	Origin
Berlenga (1995)	0.84±0.17 (17)	A	J.P.G., unpublished data
Berlenga (1996)	0.89±0.10 (11)	A	J.P.G., unpublished data
Selvagem (1991)	0.79±0.07 (9)*	A	Hamer & Hill (1993)
Selvagem (1997)	0.52±0.20 (32)	B	This study

* calculated as average proportion of chicks fed per day

Values represent means ± standard deviation, sample size in parenthesis. Different letters indicate colonies (years) that differ at $P<0.01$.

Table IV - Average nightly food provisioned (including birds not visited or not fed by parents) and coefficient of variation (standard deviation/mean*100) in the Azores, Berlenga and Selvagem islands

Colony (Year)	Start of study	Average nightly food delivery (g)	Coefficient of variation	Origin
Azores (1989)	13+24 August	61.9±50.0 (54)	80.7	Klomp & Furness (1992)
Berlenga (1996)	2 August	53.3±28.2 (126)	52.8	J.P.G., unpublished data
Selvagem (1991)	20 August	56.1±42.8 (356)	76.3	Hamer & Hill (1993)
Selvagem (1997)	22 August	52.7±68.9 (224)	130.6	This study

Values represent means ± standard deviation, sample size in parenthesis.

Figure 1. Intervals between meals delivered to Cory's shearwater chicks on Berlenga (1996, J.P.G., unpublished data) and Selvagem (1997). Sample sizes are indicated.

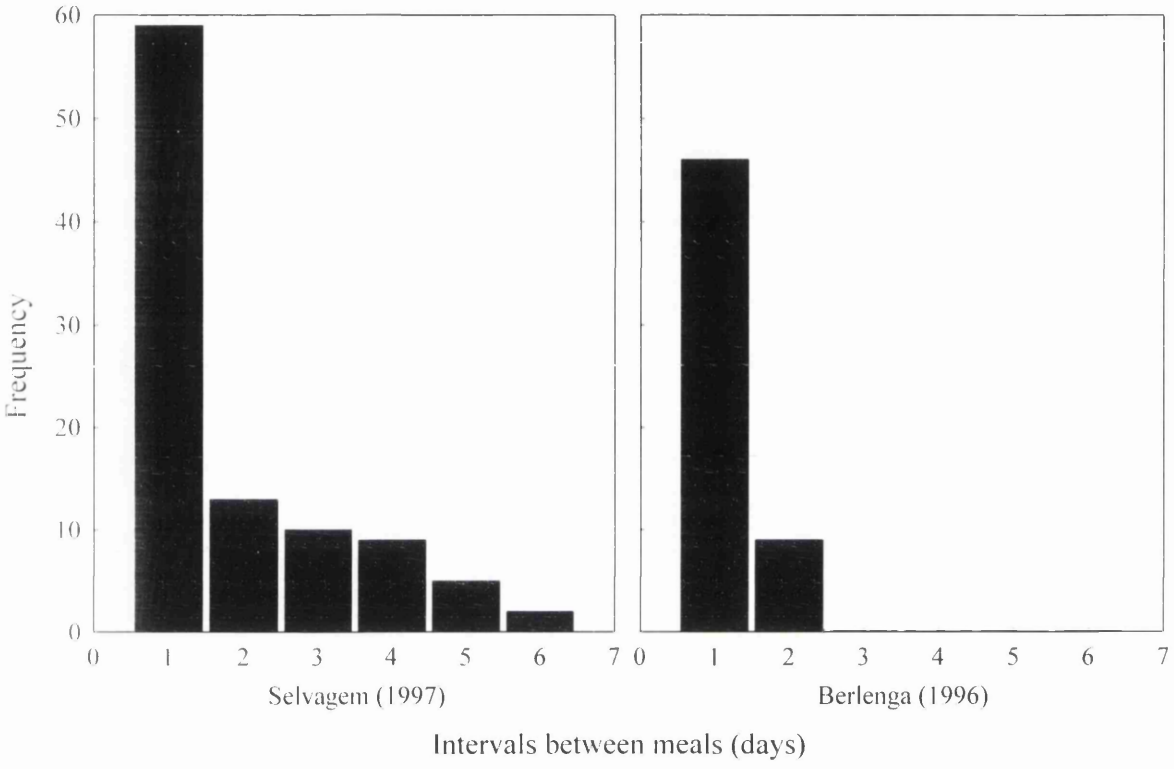


Figure 2. Intervals between meals delivered to chicks by individual birds on Berlenga (1996, J.P.G., unpublished data) and Selvagem (1997). Sample sizes are indicated.

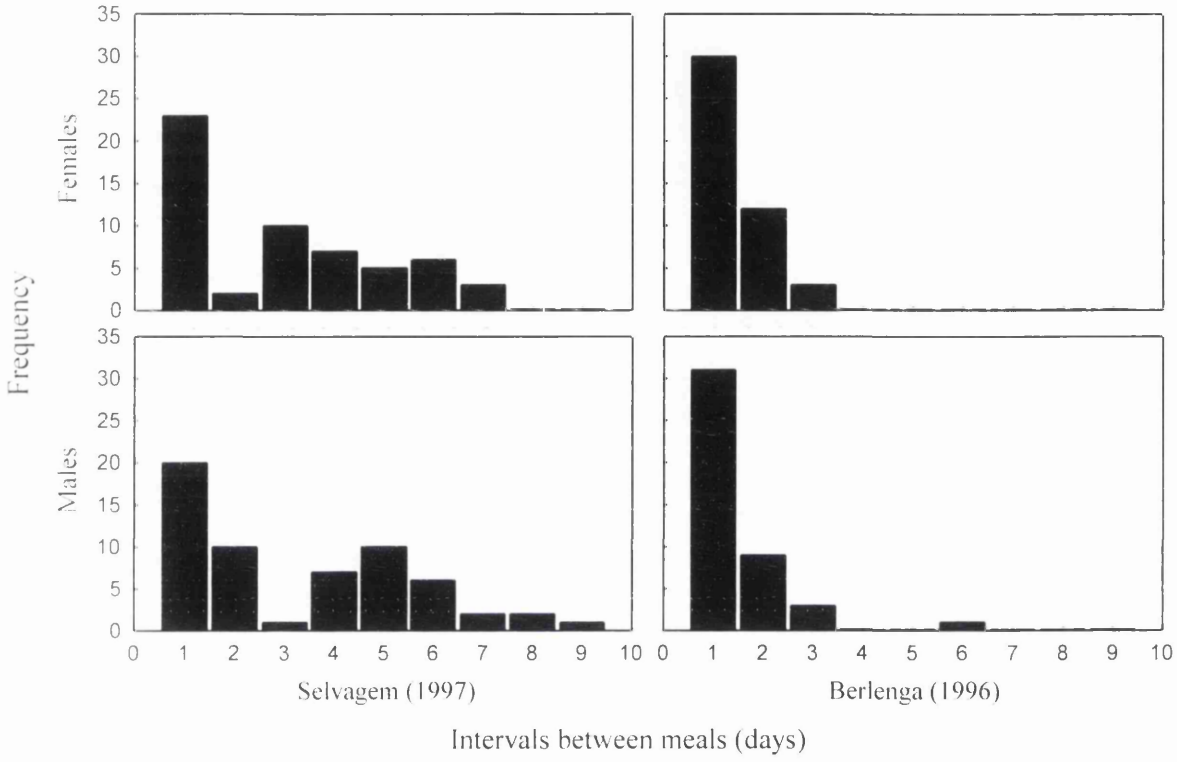
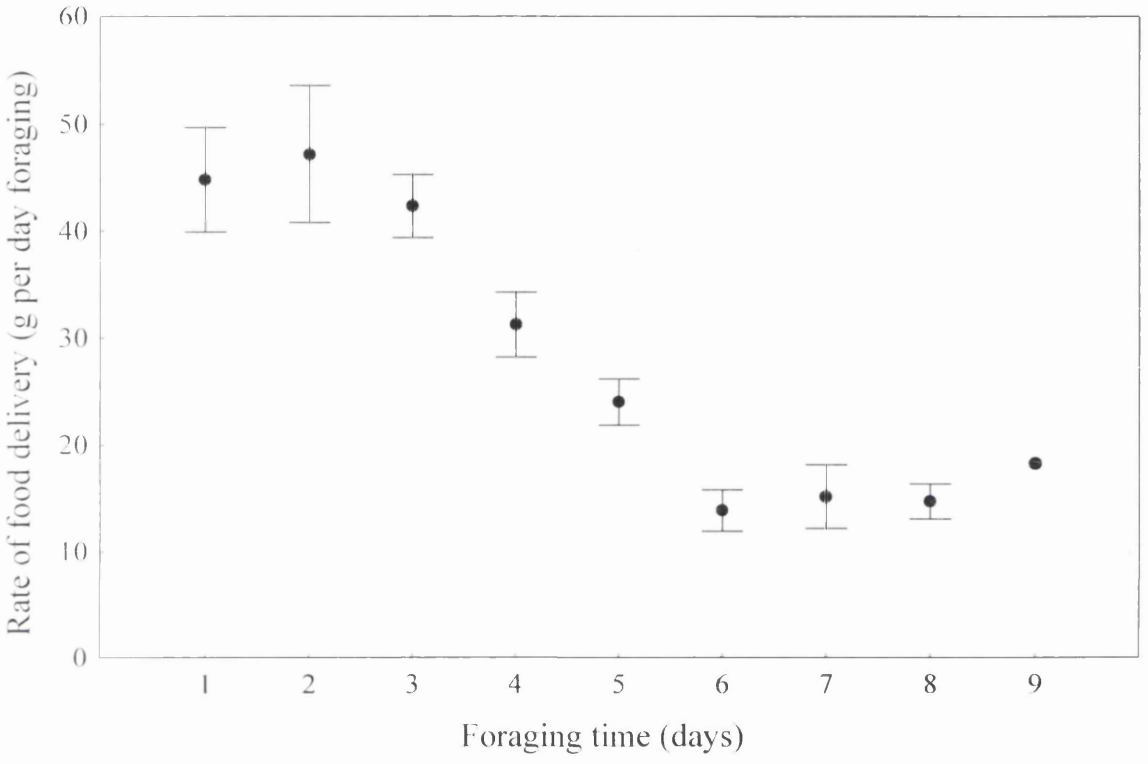


Figure 3. Amount of food per trip duration delivered to Cory's shearwater chicks by each parent on Selvagem (1997) in relation to foraging trip duration. Points represent means ± standard errors and sample sizes are indicated.



Chapter 8

Regulation of food provisioning to nestling shearwaters: why parental behaviour should be monitored?

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Summary

Temporal variation in food delivery to nestling Cory's Shearwaters *Calonectris diomedea* was examined. This was done by repeated periodic weighing during the night to test whether the magnitude and frequency of feeds were influenced by the chick's food requirements. In contrast to previous studies of chick provisioning in petrels and shearwaters, feeding evidence derived from chick weight gains was complemented by data provided by an electronic automatic system, which logged the access of each parent to the nest. Data analysed using the logging equipment showed that estimates of meal size and visiting frequency obtained from chick weighing alone were biased. The logging system combined with chick weighing also showed that, to some extent, provisioning was regulated in Cory's Shearwater, chicks left in poor condition being more likely to receive food in the following night than those left in better condition. The methods based on chick weight gains only did not detect this regulation effect. Our findings suggest that resolving parental visits to the nest is important to obtain unbiased parameter estimates, and to address the problem of regulation of provisioning rates in Procellariiformes. Our results do not support the hypothesis that accumulation of fat is just a by-product of chronic overfeeding arising due to stochastic variation in the foraging success at sea.

Introduction

Procellariiformes are renowned for their extreme life-history strategy (Warham 1990). In addition to a single-chick brood, long incubation and chick-rearing periods, all species tend to accumulate large amounts of fat during the nestling period and there has been considerable debate on the adaptive value of this phenomenon (Ricklefs *et al.* 1985). Lack (1968) suggested that fat accumulation in Procellariiformes provides an insurance against prolonged periods without food provisioning, a consequence of adults relying on pelagic food resources which are apparently scarce and unpredictable in time and space. Although some species are indeed irregularly fed (Warham 1956, Richdale 1963), most of them receive regular and frequent visits but still accumulate fat (Harris 1966, 1969, Ricklefs *et al.* 1985, Hamer & Hill 1993). Furthermore, in some species fat accumulation exceeds what would be predicted from the maximum observed periods without food provisioning (Ricklefs *et al.* 1980, Ricklefs *et al.* 1985) and most studies failed to detect regular circumstances under which these reserves were depleted due to poor feeding conditions (Ricklefs *et al.* 1985, Hamer & Hill 1993, Bolton 1995a).

The observation that fat accumulation often persists through most of the chick rearing period (Ricklefs *et al.* 1980), has subsequently led to the suggestion that it could result from "chronic overfeeding" (Ricklefs 1990, Ricklefs & Schew 1994). Since petrels generally feed their chicks at intervals of more than one day and each parent is thought to behave independently of its partner, the condition of the chick at the end of a feed does not provide a reliable assessment of its requirements at the next feed by the same parent. Instead of reacting to the short-term nutritional requirements of their chicks, adults may exhibit an intrinsic rhythm of food provisioning (Ricklefs 1992, Hamer & Hill 1993, Ricklefs & Schew 1994). In this case, if the adults just provided the necessary amount to fulfil chicks' maintenance and growth requirements, then many chicks would periodically be subjected to risks of starvation, due to stochastic variation in the foraging success of each parent. In order to minimise the probability of chance starvation, adults were expected to over-provision their chicks, so lipid accumulation should be expected (Ricklefs 1990, Ricklefs & Schew 1994).

This hypothesis implies a relatively inflexible adult provisioning rate, and it can be predicted that adults will exhibit a limited ability to respond to immediate requirements of chicks at the nest. While many studies have failed to find evidence of this short-term regulation of food delivery (Ricklefs *et al.* 1985, Ricklefs 1992, Hamer & Hill 1993, Hamer 1994, Hamer *et al.* 1997), other work has indicated that some petrel species appear to be able to adjust the level of provisioning according to the nutritional condition of the chick (Bolton 1995a, Weimerskirch *et al.* 1995, 1997, Hamer & Thompson 1997). This was only detected in species that feed their chick relatively frequently and in these cases parents can possibly obtain reliable information on chick nutritional status and efficiently act upon that information. These observations suggest that the "chronic overfeeding" hypothesis is not appropriate to explain fat accumulation in all Procellariiform species.

Most studies examining the existence of regulation of food provisioning have been conducted on nocturnal small or medium-sized seabird species and involve the description of natural variation of meal sizes and feeding frequency (Ricklefs 1984, Ricklefs *et al.* 1985, Thompson 1987, Schaffner 1990a, Hamer & Hill 1993, Hamer 1994, Bolton 1995a, Shea & Ricklefs 1996, Hamer & Thompson 1997). Alternatively, predictions of models of provisioning control were tested by experimental studies, where the foraging ability of adults or the nutritional status of the chicks were artificially manipulated (Ricklefs 1987, 1992, Hamer & Hill 1994, Bolton 1995b, Mauck & Grubb 1995, Weimerskirch *et al.* 1995, 1997, Schreiber 1996). The former approach generally followed a protocol proposed by Ricklefs *et al.* (1985) based on periodic weighings of chicks, usually during the night. Meals (calculated as the sum of the positive weight variations between intervals) are assigned to the presence of one or two birds on the basis of the magnitude of weight variation, by assuming that parents are visiting the nest independently and at the same rate and that the higher weight gains correspond to meals delivered by two adults (Ricklefs 1984, Ricklefs *et al.* 1985).

Schaffner (1990b) mentioned that in some cases there could be a considerable disagreement between the patterns of adult attendance deduced on the basis of weight increments of the chicks and from direct observational procedures. However, no studies have quantitatively addressed the effects that the process of assigning meal size to feeds by one or both parents can produce on the ability to detect the hypothesised feeding regulation and related estimates (meal sizes, feeding frequencies, interval between meals). In fact, the magnitude of these effects and the circumstances under which they are likely to produce a serious bias to the variables being estimated remain unclear. Critical assessment of such biases requires a comparative analysis of periodic weighing data obtained from standard analysis as developed by Ricklefs *et al.* (1985) and that arising from an independent assessment of parental attendance.

Cory's Shearwaters *Calonectris diomedea* (Scopoli) is a pelagic Procellariiform, breeding in north-east Atlantic islands and in the Mediterranean (Cramp & Simmons 1977). The Atlantic race *C. diomedea borealis* breeds in large numbers in Madeira, Azores and Canary archipelagos and also off the Portuguese coast (Cramp & Simmons 1977, Hagemeijer & Blair 1997). Klomp & Furness (1992) and Hamer & Hill (1993) have examined the natural variability of meal size and feeding frequency of this species in the Azores and on Selvagem Grande (about 300 km south of Madeira), respectively. It has been suggested that the presence or absence of regulation can be related to the overall feeding periodicity (Hamer 1994, Hamer & Thompson 1997). Consequently, the comparison of colonies where birds exhibit differing feeding periodicity would shed light on the proposed relationship between the frequency of food delivery to the nest and the ability to regulate food delivery.

In this paper, we compare the estimates of meal sizes of Cory's Shearwater obtained from standard methods described by Ricklefs *et al.* (1985), where parental presence is deduced from weight variations of the chick, with those provided by an independent monitoring of parental nest attendance, using activity recorders. We examine whether in the study population there is evidence of adjustment of provisioning according to

the short-term requirements of the chicks, and we compare the performance of each method in detecting it.

Methods

This work was carried out on Berlenga Island (39°24'N, 9°30'W), Portugal, where about 120 pairs breed in burrows and rock crevices (Granadeiro 1991). At this colony, birds are strictly nocturnal ashore during the chick rearing period, and visit the nests frequently (Granadeiro *et al. in press* a).

Nineteen chicks were selected on a study plot on 2 August 1996, weighed at 19.00 hours, local time (using an electronic balance, accurate to 1 gram) and their wings measured (to the nearest mm). These chicks were subsequently weighed at 6-hours intervals (01.00 hours, 07.00 hours, 13.00 hours and again at 19.00 hours) each day, until 11 August. At the beginning of the study some small chicks were still brooded by one adult, and these were excluded from the analysis until left alone at their burrows during the day. The hatching date could not be not determined, so we estimated these dates from wing measurements, which predicts age to ± 2 days (Granadeiro 1991). The weighing protocol was repeated again from 9 to 16 September 1996 at 20 nests, when some chicks have reached their peak weight. In this period, all weighings were made one hour later, to account for differences in the time of sunset and sunrise. On each occasion, chicks were weighed in the same sequence and the procedure took about 1 hour to complete. None of the chicks regurgitated any food or oil during handling. Adult birds did not seem particularly disturbed by our presence during the night, and frequently stayed inside the burrow during the nocturnal weighings, and eventually continued feeding their chicks.

Some study burrows (14 in the first period and 12 in the second) were equipped with a logging equipment, designed to detect and identify the sex of each visiting adult (see Granadeiro *et al.* (*in press* a) for a full description of the system). Adult birds were captured by hand before egg laying, sexed on the basis of their vocalisations or measurements (Granadeiro 1993) and equipped with a magnet on a tail feather to

enable detection by the electronic logging system. The movement of the magnet through the detection unit (a PVC tube, placed at the entrance of the burrow) was recorded by the logging system as: nest number, date, time, sex-specific coding, duration of the movements (Granadeiro *et al. in press* a). The detection units were installed in mid-April, and at the start of this study, birds were familiar with presence of this equipment at the nest. Males and females at logged nests were marked with a distinctive paint spot on the forehead, to allow easy identification without handling. All occasional observations of marked individuals at these burrows during the nocturnal weighings matched the information provided by the logging equipment, and no chick increased its weight without an adult being logged at the nest. We are therefore confident that we correctly identified arrivals and departures by each member of the pair and especially that no bird visited the nest without being detected. In fact, the system was extensively tested for reliability, and the likelihood of not detecting a marked bird visiting its nest is negligible (Granadeiro *et al. in press* a). In this paper, we used the term "meal" to refer to the total amount of food delivered by either parent overnight, and "feed" to refer to the amount of food received from a single adult.

Quantifying meal sizes

The amount of food received by a chick during the night was calculated as the sum of the weight increments between repeated measurements (hereafter referred to as SUM, following Ricklefs *et al.* (1985)). However, this procedure underestimates the total food given by parents, since chicks lose weight between weighings, as a result of excretion and respiration. Ricklefs *et al.* (1985) calculated the average bias using the expression $i(l_1+l_2)/2$, where i is the interval between weighing and l_1 and l_2 are the rates of weight loss before and after a meal. This correction was applied due to a lack of relationship between these rates and either age or mass of chicks and size of feeds in Ricklefs *et al.* (1985) study of Leach's Storm Petrels *Oceanodroma leucorhoa*, as found in other species (e.g. Hamer & Hill 1993, Lorentsen 1996). In this study we calculated this amount for each period and we added it to each positive value of SUM, and we refer to this procedure will be referred to as **"Add Error"** method.

More recently, it has been showed that in some species there were linear relationships between the rates of weight loss before and after a meal and age, initial chick mass and size of the meals delivered (Bolton 1995a, Hamer & Thompson 1997, Hamer *et al.* 1997). These relationships were used to estimate the weight loss between the initial and final weighing, assuming that feeding occurred midway between weighings. The correction was applied only when a weight increase was identified. Although small meals would fail to be detected, they were expected to occur with a negligible frequency (Ricklefs *et al.* 1985). This procedure will be referred to as **"Correcting SUM>0"** method.

Assigning single and double feeds to weight increments

In these two methods, we used the protocol proposed by Ricklefs (1984) for assigning each SUM value to a meal delivered by one or two adults. The probability that a parent will fail to feed its chick (**q**) can be estimated from the observed proportion of chicks that were not fed, which equals $\mathbf{q^2}$. The proportion of chicks likely to have received one or two meals can be estimated as $\mathbf{2x(1-q)xq}$ and $\mathbf{(1-q)^2}$, respectively. These computations require that parents are feeding their chicks independently, and with similar probabilities. SUMs estimated by each method were ranked and double meals were attributed to the higher values and single feeds to the lower values, on the assumption that all increments resulting from a double feed would be greater than those produced by a single feed (Ricklefs 1984). In the "**Logging system**" method, we used the same values of SUM as calculated for "Correcting SUM>0" method, but meals were classified according to the number of birds known to have visited each nest, as obtained from the logging system.

Calculation of an index of body condition

In the first period (August), we calculated a daily index of condition for each chick, based on the linear regression of weight over age. This index was calculated from the residuals, expressed as a proportion of the predicted value, following Hamer & Hill

(1993) and Bolton (1995a). Condition was not computed for the second period, since most chicks had reached their peak weight, and so there was no correlation between weight and age over this period.

Statistical analysis

Statistical comparisons between methods were performed in relation to data provided by the logging system, on the basis that we considered that the latter method correctly attributed the presence of just one adult to single feeds, even though, in some cases, the detection of two birds at the nest (using the logger) may not correspond to a double feed.

The data analysed in this paper represent repeated measures over the same individuals during a long period. To avoid effects of pseudo-replication (Hurlbert 1984) due to non-independence of the data, we calculated test statistics on averages for individual chicks, where appropriate, and followed Zar (1996). Throughout this chapter we present means±standard deviations, except where otherwise stated.

Results

Computations of weight correction

In this study the corrections introduced to the SUM values in the "Add Error" method were 14.5 gram in the first period and 20.0 gram in the second (average rate of weight loss before and after a meal of 2.18±1.22 $g.h^{-1}$ (n=108) and 2.64±1.14 $g.h^{-1}$ (n=98) for the first period and 2.98±1.78 $g.h^{-1}$ (n=113) and 3.69±2.28 $g.h^{-1}$ (n=24) for the second period, respectively).

For the other methods, we tested both linear and non-linear relationships of rates of weight loss with age, initial weight and meals size (where appropriate) and the former always provided the best predictors. Rates of weight loss ($g.h^{-1}$) before a meal were

linearly related to initial weight of chicks (in g) and with age (in days) by the equations:

First Period:

(1) Weight loss=1.0×10^{-2} x Initial Weight - 14.3×10^{-2} x Age +0.45

r^2=0.27, n=108, P<0.0001

Second Period:

(2) Weight loss=0.65×10^{-2} x Initial Weight-5.8×10^{-2} x Age +6.30

r^2=0.23, n=107, P<0.0001

Rates of weight loss ($g.h^{-1}$) after a meal were related to initial weight and meal size (both in g). Age was also a significant predictor of rate of weight loss in the first period, while it was not included in the multiple regression in the second. The relationships are:

First period:

(3) Weight loss = 6.76×10^{-3} x Initial weight + 8.46×10^{-3} x Meal size - 0.78×10^{-3} x Age + 0.669

r^2=0.23, n=98, P<0.0001

Second period:

(4) Weight loss = 0.62×10^{-2} x Initial weight + 8.46×10^{-3} x Meal size - 4.98

r^2=0.50, n=24, P<0.001

The corrections applied to the initial and final weighing using these relationships averaged 15.0±5.9 g (n=161, range 2.7-28.9 g) in the first period and 24.1±14.1 g (n=141, range 1.0-71.3 g) in the second ("Correcting SUM>0" and "Logging system"

methods). Although these values are relatively close to those calculated following Ricklefs *et al.* (1985), the magnitude of the correction factor varied considerably, depending on the weight, age and size of the meal (where appropriate).

Patterns of food delivery

We examined the patterns of food delivery by dividing the chick age into 10-day classes in both periods, following Bolton (1995a). For each class, we regressed the overnight food delivery upon net 24-hour weight change (dusk weight on night $n+1$, in relation to dusk weight on night n), hereafter referred to as NET (Ricklefs 1984). The intercept on the Y-axis was taken as the food requirement for zero growth. In this analysis, we used values of SUM corrected according to "Correcting SUM>0" and "Logging system" methods.

During our study, chick requirements increased with chick age, up to the age of 50 days (*ca.* 50% of the chick development period), and did not vary significantly afterwards (Fig. 1). The average amount of food delivered to chicks increased up to the age of 30 days and stabilised between age 40 and 60 days. These data include occasions when no food was delivered and therefore represent the average mass of food received by chicks. There were significant differences in the nightly food delivery according to the age of chicks (Kruskal-Wallis $H_{4,\ n=66}=16.9$, $P=0.002$). Non-parametric post hoc tests revealed that differences were restricted to food delivered to chicks aged 21-30 days in relation to age classes 1-10 days and 51-60 days. Overall, the average rate of food delivery was 76.1 g chick^{-1}.night^{-1} in the first period and 58.7 g chick^{-1}.night^{-1} in the second period.

NET weight change increased during the first period of study (chick age up to 30 days) and was close to zero in the second period (chick age 40 to 60 days - Fig. 1). This corresponded to an average growth of 23.6±4.4 g.day^{-1} (n=19) in the first period (average slope of the regression of weight over age, for each chick) and -9.3±11.1 g.day^{-1} (n=20) in the second period. There were no significant differences between the age-specific average chicks weight in a previous year (Granadeiro 1991) and those

obtained in this study (Two-way ANOVA, with age-class and year as factors: for effect of year, $F_{1,135}$=1.14, P=0.288), indicating that the weighing protocol had no adverse influence on growth.

Meal sizes, feeding frequencies and intervals between meals

Table 1 presents the estimated (observed in "logging system" method) number of chick-nights when nought, one or two adults were present, as obtained from application of the different methods. In September, the methods "Add error" and "Correcting SUM>0" produced a significantly different pattern of adult attendance in relation to that obtained with the logging equipment (Table 1), and in August the comparison was not significant. Not all parental visits were associated with chick weight gains. These non-feeding (or low-feeding) visits occurred in 4.1% (n=118) and 20.3% (n=69) of the chick.nights, in the first and second period, respectively. Even when these non-feeding visits were excluded from the analysis, there was a considerable disagreement between the number of adults known to have visited their nest each night, and the corresponding classification provided by alternative indirect methods. Combined misclassification rates were greater than 30% in single and double visits (Table 2).

Feeding frequency, defined as the proportion of chicks that increased their weight during the night, was 0.95±0.08 day^{-1} (n=14) in the first period, and 0.78±0.16 day^{-1} (n=12) in the first and second periods, respectively. Meals provided by a single adult or by two adults in August and September are presented in Table 3. On some occasions, adults were detected at the nest, but chicks did not increase their weight and these situations were not considered in the following analysis. In the first period, the estimates of single and double feeds provided by the logging system were significantly different from those obtained from the indirect methods (except double feeds in the "Add error" method). Similar differences were found in the second period (Table 3).

Regulation of feeding

We examined the relationship between the condition of chicks after a meal and the subsequent feeding history. An index of condition could not be calculated in the second period (see methods) and we restricted this analysis to data obtained in the first period (August), when regulation effects are more likely to be detected (Hamer & Hill 1993, Bolton 1995a). We calculated the relationship between body condition after a double visits (following Hamer & Hill (1993) and Bolton (1995a)) and the size of the next meal, according to each method. In none of the methods did we find a significant correlation between these two variables (all Spearman rank correlations not significant), suggesting that the overall magnitude of the meals was not regulated according to the nutritional status of the chicks. We did not relate condition of chicks after a double meal with interval to the next meal because all monitored nests were visited by at least one adult.

We also examined the condition of chicks after being visited by two adults on night *n*, in relation to the number of visits received on the following night (Table 4). By using the logging equipment, we found a significant difference between chicks in good and poor condition in terms of number of feeds received on the night following a double visit. Chicks that were left in comparatively poorer condition were more likely to receive visits from two adults than those left in better condition (Table 4). This suggests that the nutritional status of chicks may influence the subsequent pattern of food delivery by parents. These differences were not detected by any of the alternative methods (Table 4). These tests were calculated on averages per individual chicks in order to avoid the effects of pseudoreplication (Hurlbert 1984). In the absence of this correction, if we include all data from the chicks, the regulation effect would still be significant ($P<0.005$) using the logging equipment, but again would fail to be detected using any of the alternative methods.

The amount of food eaten at each feed can also be influenced by the chicks' nutritional status. Chicks in good condition may not consume all the food brought by their parents. In this study, the condition at dusk was not related to the size of single feeds (Table 5). However, this relationship was significant and negative for double feeds, according to data from "logging system", suggesting that chicks in poor condition will accept all the food brought by their parents, whereas those in better condition will not (Table 5). The other two methods did not detect this effect.

Discussion

We found no evidence that the periodic weighing protocol had any influence upon the behaviour of adults in terms of rates or amount of food provisioning. None of the adults occasionally present at the burrows during the weighings seemed particularly disturbed by the careful removal of the chicks from the nest. Furthermore, age-specific chick weight did not differ significantly from that recorded in previous years at the study colony (Granadeiro 1991). Hamer & Hill (1993) and Granadeiro *et al.* (*in press* b) also failed to detect any adverse effect of these nocturnal weighings on the rates of food provisioning of Cory's shearwater, and this agrees with a number of studies on other Procellariiform species (e.g. Hamer 1994, Bolton 1995a, Minguez 1996, Hamer & Thompson 1997, Hamer *et al.* 1997).

Attendance and meal size estimates

There was a considerable disagreement between the inferred patterns of adult attendance resulting from applying the "blind weighing" methods alone and those obtained from logging visits of adult birds. Hence, chick weight gain can only be used to ascertain feeding events, and will fail to provide reliable information on parental visiting patterns. The "blind weighing methods" will not resolve both non-feeding visits, and visits resulting in the provision of small meals, which would only be detected using very frequent chick weighings. However, even when non-feeding visits (i.e. visits not associated with a detectable weight increase) were excluded from the analysis, there was a strong disagreement between methods in the attribution of adult

presence to daily weight increments. In our study, about 14% of the meals thought to correspond to double feeds were in fact associated with the presence of just one adult, and this is a tangible bias in Ricklefs *et al.* (1985) method. Since the rationale of these methods is strongly dependent on the correct assignment of each weight increment to 0, 1 or two adults most of the subsequent computations differed from those obtained from the logging system.

Differences in assignment of adult presence to weight increments are mainly a consequence of a particular assumption of the method proposed by Ricklefs *et al.* (1985): larger SUMs correspond to the presence of two adults, and smaller meals to food delivered by one adult. The subsequent step is to truncate the ranked values of SUM, allocating the highest SUM values to the predicted number of double visits and the other to single meals. The distribution of SUMs is usually not bimodal (e.g. Ricklefs 1984, Ricklefs *et al.* 1985, Hamer & Hill 1993). Under the assumption of some degree of overlap on the (assumed normal) distributions of single and double feeds, we would predict that this discrimination method would underestimate single feeds (large single feeds would be classified as double feeds) and overestimate double feeds (by excluding small double feeds). The magnitude of these biases would tend to increase with increased variance in single and double feeds. The effects of misclassification would also be enhanced if the difference between single and double feeds decreases. For example, if chicks visited by both parents accept less food from the second than from the first adult, the overlap in the distribution of single and double feeds will be increased, and consequently more feeds will be incorrectly assigned.

The results obtained from the activity logger match well with the above predictions. In both periods single and double feeds were systematically under- and overestimated, respectively. Again, although it can be argued that logging double presence at the nest do not necessarily imply that chicks were feeds by both adults (an effect that would lead to double feeds being underestimated), but it should be stressed that overestimated double feeds are an expected outcome of Ricklefs *et al.* (1985) methodology. Moreover, weight increments associated with the presence of just one

adult are clearly single feeds, and our results suggest that these feeds can be underestimated by up to 30% (Table 3). This effect was particularly clear because apparently chicks were not accepting all the food load when visited by both adults on the same night (Table 5). Rejection of large meals were also observed in British Storm-Petrel *Hydrobates pelagicus* (Bolton 1995a), and Black-browed albatross *Diomedea melanophris* (Weimerskirch *et al.* 1997), and it probably occurs in other Procellariiform species. This "satiation" effect was only detected using attendance data provided by the activity logger, and none of the methods based only in weighings was sensitive to it.

It is also worth stressing that studies adopting the "blind weighing" methodology have used the fact that double feed estimates should be close to twice single feeds as a validation rule for correct judgement of meals provided by one and two adults (*e.g.* Ricklefs *et al.* 1985, Hamer & Hill 1993, Bolton 1995a, Minguez 1996, Hamer & Thompson 1997). This was further supplemented by a similar relationship between variances of double and single meals. In our study, these conditions were reasonably met in "Add Error" and "Correcting SUM>0" methods (the most frequently used methods in the literature) in both periods (Table 3), despite the marked differences in meals size estimates. Consequently, the "blind weighing" methodology can yield the above relationships between means and variances but still fail to provide accurate estimates of meal sizes.

Regulation of food provisioning

In our study we found some evidence of regulation of food delivery of Cory's shearwater in accordance with short-term requirements of chick by using the logging equipment, but such an effect was not detected by any of the indirect methods. The results analysed using this novel logging technique suggest that to some extent the condition of chicks can influence the subsequent patterns of food delivery by the adults. The regulation appears to operate at the level of feeding frequency and not feeds size, as in other species (Bolton 1995a, b, Weimerskirch *et al.* 1997). This effect was detected despite the use of a conservative statistical approach, which consisted in

analysing only the average condition of each chick according to the subsequent feeding history (two, one or no meals provided), which greatly reduced the number of degrees of freedom of the comparisons. If instead, we included all data in the analysis, in a comparable way to previous studies (*e.g.* Hamer & Hill 1993, Hamer 1994, Bolton 1995a), we still would have found a significant effect using the logger and again fail to detect evidence of regulation with the remaining weighing procedures.

Our findings indicate that, at least under certain circumstances, the established "blind weighing" methodologies can fail to detect some evidence for regulation of food provisioning. One possible cause for such an effect is that the starting-point for one of the tests examining the influence of chicks in determining rates of provisioning is the condition of chicks *after* a double visit (to control for the probability of being fed). Since double feeds are *a priori* attributed high meal values there will be a considerable reduction in the variability of chick condition and so discrete effects can fail to be detected.

Hamer & Hill (1993) did not find indications of regulation of food provisioning in Cory's Shearwater at Selvagem Island. In our study parents were visiting the colony very frequently, and had more opportunities for accurate assessment of chick requirements. It is plausible that under these circumstances chicks exerted a significant influence on the provisioning behaviour of their parent, either through begging intensity or frequency or from other yet undescribed mechanism. However, comparability of our results may be compromised by the fact that generally previous studies did not monitor adult presence directly and so our results can not be used as supporting evidence that the presence or absence of regulation is related to the overall feeding periodicity.

Our results analysed according to the methods used in the same species by Hamer & Hill (1993) in the Selvagem and Klomp & Furness (1990) in the Azores ("Add Error" method) yield compatible values for average rates of food delivery (56.1 g chick^{-1}

$^{-1}$.night^{-1} in the Selvagem and 61.9 g chick^{-1}.night^{-1} in the Azores) to those obtained in this study, although meal sizes and feeding frequency were different.

There is accumulating evidence that some Procellariiformes have some ability to adjust their provisioning rate in relation to short-term requirements of chicks (e.g. Bolton 1995a, b, Hamer & Thompson 1997, Weimerskirch *et al.* 1997). These observations cast some doubt on the hypothesis that lipid accumulation in this group is just a by-product of chronic overfeeding, as suggested by Ricklefs & Schew (1994). As we have shown, at least under certain circumstances, the current methods of assessing aspects of the feeding behaviour based on chick weight gains can provide rather inaccurate estimates of meal size and visiting patterns. These methods can also fail to detect evidences of regulation of food provisioning, which is a key-aspect to understand the extent to which life-history adaptations are linked to energetic constraints arising from the postulated scarcity and unpredictability of food resources in the pelagic marine environment. There is clearly need to use more accurate data on adult attendance, combined with chick weighing to correctly evaluate whether feeding is regulated in most petrels and shearwaters and the extent to which this feature depends on the overall feeding frequency.

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Table 1. Number of chick-nights with no visits, visits by 1 or by 2 adults, according to different methods in the first and second periods.

	First period		Second period	
	Logging System	**Add Error and Correcting SUM>0**	**Logging System**	**Add Error and Correcting SUM>0**
No visits	0	7	3	33
One adult	38	54	38	73
Two adults	80	103	31	41
		$\chi^2_2 = 5.31$		$\chi^2_2 = 13.30$
		P=0.07		P=0.001

Table 2. Percentage of incorrectly classified single and double feeds, estimated from chick weight gains only ("Add Error" and "Correcting SUM>0" methods), in relation to data obtained from logging parental presence in August (First period) and September (Second period). Visits detected by the logging system, but not associated with weight gains by chicks were excluded from this analysis.

	First period		**Second period**	
	Add Error	**Corr. SUM>0**	**Add Error**	**Corr. SUM>0**
Single feeds	17.0%	17.8%	29.1%	30.9%
Double feeds	13.4%	14.3%	14.5%	14.5%
Total	30.4%	32.1%	43.6%	45.4%

Table 3. Estimates of single and double feeds (averages per nest, in g, means±SD, sample size in parenthesis) in the first and second periods, according to different methods of assessing adult presence. Paired tests were performed in relation to data obtained with the logging system, and were based on paired observations from each nest (for explanations, see text).

First period (August)

	Logging System	**Add Error**	**Correcting SUM>0**
Single feeds	62.2±12.9 (10)	48.0±6.0 (18)	46.6±9.5 (18)
Paired *t*-tests	---	t_9=3.7, P=0.005	t_9=4.6, P=0.001
Double feeds	83.3±15.5 (14)	88.9±12.3 (19)	90.5±11.5 (19)
Paired *t*-tests	---	t_{13}=-1.8, P=0.089	t_{13}=-2.5, P=0.029

Second period (September)

	Logging System	**Add Error**	**Correcting SUM>0**
Single feeds	72.9±31.4 (12)	55.7±9.7 (20)	57.5±12.0 (20)
Paired *t*-tests	---	t_{11}=2.8, P=0.017	t_{11}=2.5, P=0.030
Double feeds	81.4±41.0 (8)	111.9±16.6 (18)	128.6±19.6 (18)
Paired *t*-tests	---	t_7=-1.9, P=0.088	t_7=-3.7, P=0.007

Table 4. Condition of chicks (average per chick, means±SD, sample size in parenthesis) following a double in relation to subsequent feeding history. One-tailed Paired *t*-tests tests were performed on paired observations from each nest (for explanation, see text).

Number of feeds on night *n+1*	**Logging system**	**Add Error**	**Correcting SUM>0**
No visits	---	0.249±0.081 (2)	0.207 (1)
1 Adult	0.259±0.144 (11)	0.241±0.153 (15)	0.250±0.173 (14)
2 Adults	0.184±0.161 (12)	0.254±0.154 (18)	0.250±0.153 (17)
Paired *t*-tests	t_8=2.35, *P*=0.023	t_{13}=-0.49, *P*=0.316	t_{11}=0.64, *P*=0.269

Table 5. Relationship (Spearman rank correlation) between chick condition at dusk and amount of food delivered, in relation to number of visits by parents in the first period (August).

	Logging System	**Add Error**	**Correcting SUM>0**
One Adult (single feeds)	r=0.06, n=38 P=0.719	r=-0.13, n=54 P=0.332	r=0.079, n=54 P=0.240
Two Adults (double feeds)	r=-0.24, n=80 P=0.033	r=-0.19, n=103 P=0.052	r=-0.042, n=103 P=0.672

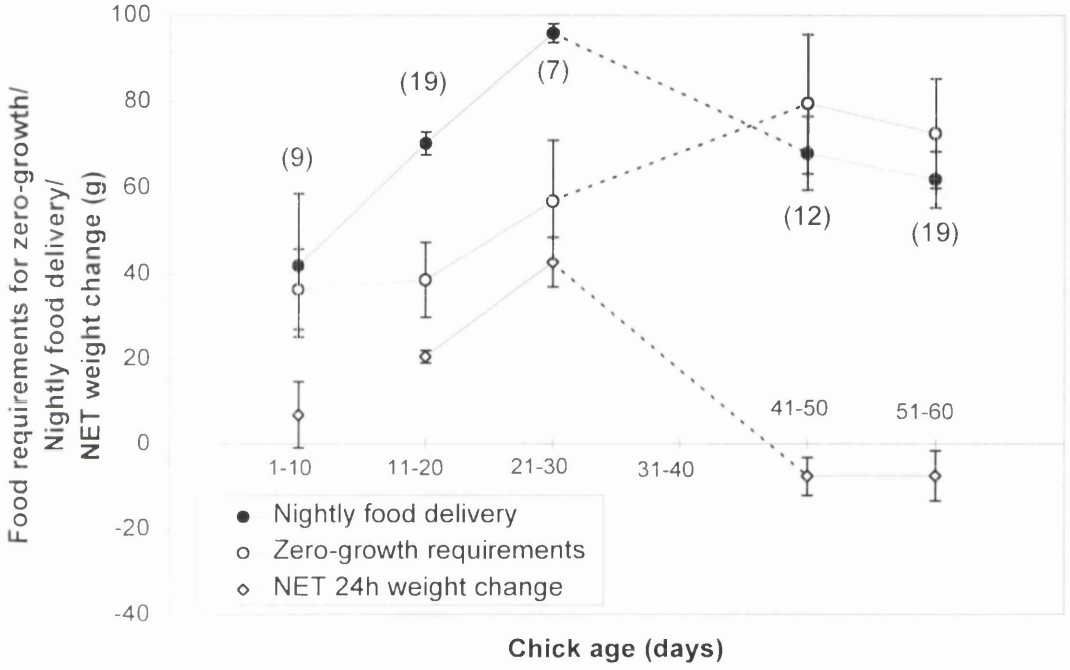

Fig. 1. Variation in overnight food delivery (zero feeds included), food requirement for zero growth, and NET 24 h weight change. Points represent means±SE and sample sizes are indicated.

Chapter 9

Response of Cory's shearwater Calonectris diomedea to experimental manipulation of chick condition

The spatial and temporal variability of food resources in the marine environment is considered to represent a major factor determining life-history traits of seabirds (Lack 1968). During the breeding season, seabirds are constrained by the need to visit their nests regularly (e.g. to carry out incubation or feed their brood), and during the same period to obtain food both for themselves and for the chicks, with an unpredictable level of success. This is particularly true for procellariiform species (albatrosses, shearwaters and petrels), many of which extensively forage in oceanic waters that often exhibit low biological productivity (Ashmole 1971, Warham 1996). Procellariiformes lay a single egg clutch, and the semi-precocial chick growth at a comparatively low rate. These traits were initially considered to be related to low foraging success at sea due to unpredictability of food resources (Lack 1968) , and the observation that chick accumulate large amounts of fat during its development suggest that food supply is severely limited in this group. However, most recent studies have acknowledged that persistent unfavourable oceanographic conditions, resulting in prolonged periods without any parental visits to the nest, are relatively infrequent (Ricklefs et al. 1985, Hamer & Hill 1993, Hamer et al. 1997). Additionally, as in other groups of seabirds (e.g. Taylor & Konarzewski 1989) the magnitude of fat accumulation by Procellariiformes chicks is apparently in excess of that needed to withstand normal fasting periods (Ricklefs et al. 1980). These observations have cast doubts on the view that such developmental traits were directly connected to the postulated scarcity and unpredictability of food resources at sea (e.g. Ricklefs et al. 1985, Hamer 1994, Ricklefs & Schew 1994, Bolton 1995a, Mauck & Grubb 1995).

Considerable attention has been paid to examining natural patterns of food delivery to nestling petrels, as a means to determine proximate controlling factors for their rates of food delivery (Ricklefs et al. 1985, Schaffner 1990, Hamer & Hill 1993, Bolton 1995a, Hamer et al. 1997, Weimerskirch et al. 1997a, b). Additionally, several experimental studies have examined the parental provisioning response following an experimentally induced decrease in their foraging ability (Sæther et al. 1993, Mauck & Grubb 1995, Weimerskirch et al. 1995), or after manipulation of chick demands at the nest (e.g. Ricklefs 1987, 1992, Hamer & Hill 1994, Anderson et al. 1995, Bolton

1995b, Schreiber 1996, Weimerskirch et al. 1997b). The results of this experimental work revealed marked differences in the ability of different species to respond to changes in reproductive demands. Indeed, while in some species adults were able to adjust their effort in response to changes in chick demand (Bolton 1995a, Weimerskirch et al. 1995, 1997b), other species appeared to follow a relatively inflexible provisioning rate (Ricklefs 1987, 1992, Hamer & Hill 1994). Similarly, brood enlargement experiments have provided ambiguous evidence, in relation to the parental adjustment to offspring needs in seabirds (review in Ydenberg & Bertram 1989, Schreiber 1996). This diversity in parental response casts doubts on the existence of a single mechanism through which Procellariiformes may regulate food provisioning (Weimerskirch et al. 1997a).

It is now believed that in many species offspring solicitation behaviour conveys information on their current needs (Kilner 1995, Cotton et al. 1996, Kilner & Johnstone 1997, Ottoson et al. 1997). Parents are apparently able to perceive the nutritional status of their chicks and can increase their provisioning rate accordingly (Mondloch 1995, Ottoson et al. 1997). Seabirds represent a particularly adequate group to address hypothesis relating levels of chick signalling to parental response. Indeed, many species lay a one-egg clutch, and usually nest in islands where predation levels are usually low. Therefore, models of solicitation-induced provisioning can be analysed without the complexities arising from sibling competition (Briskie et al. 1994, Godfray 1995, Kalcenik et al. 1995) and costs due to increased risks of predation (Haskel 1994, Leech & Leonard 1997, Halupka 1998). In this context, the importance of begging behaviour as a means of providing information on current nutritional status of chicks has been recognised in some seabird species (e.g. Impekoven 1971, Henderson 1975, Harris 1983). However, the evidence for effective use of this type of signalling among Procellariiformes is still scant. Ricklefs (1992) did not record any relationship between chick condition and vocal response to handling (which he assumed to reasonably match begging behaviour) in Leach's Storm petrel Oceanodroma leucorhoa chicks. If Procellariiformes do not respond to chick begging calls, either this behaviour does not

convey any meaningful information on the nutritional status of chicks, or parents are unable to respond to it (Hussel 1991, Ricklefs 1992).

The decisional processes by which petrels determine their levels of provisioning are still poorly understood, but recent studies suggest that adult condition plays a central role in those regulation processes (e.g. Chaurand & Weimerskirch 1994, Lorentsen 1996, Weimerskirch et al. 1997b, Weimerskirch 1998). In some species, the duration of a given foraging trip depends on the condition of the parent at the end of the previous one (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, 1997a, b, Ricklefs & Schew 1994, for a model). This emphasises the need to examine the behaviour of individual adults and not simply the delivery rate experienced by chicks at the nest (Weimerskirch et al. 1997a).

Cory's shearwater Calonectris diomedea, is a pelagic Procellariiform breeding on sub-tropical North East Atlantic islands and in the Mediterranean (Cramp & Simmons 1977). The aims of this study were to examine the extent to which breeding shearwaters were able to adjust the rates of food provisioning in response to manipulated chick demand at the nest. Additionally, we tested whether begging behaviour was related to current chick needs. We adopted an experimental protocol, where two groups of chicks experienced opposing manipulation of their body condition. One group was given a food supplement, while the other group was deprived of part of the food provisioned by their parents. We examined the response of parents to these manipulations, in terms of changes in amount of food delivered, and by variation in feeding frequency by each adult. Furthermore, we analysed the changes in the begging behaviour of chicks, under these contrasting treatments.

METHODS

Fieldwork was carried out on Selvagem Grande island (30°09'N, 15°52'W, situated approximately 300 km south of Madeira), between 12 August and 4 September 1997. The breeding population of Cory's shearwater on Selvagem Grande (hereafter referred to as "Selvagem") is currently estimated at 13 000 pairs (Mougin et al. 1996a). Hatching is relatively synchronous and most chicks hatch between 18 and

31 July (Granadeiro 1991). On 12 August, 32 burrows of Cory's shearwater with a single chick were randomly selected and equipped with an automatic detector, which logged all movements of adults in and out of the burrows (see Granadeiro et al. (in press a) for details on system design and reliability). The detection units, placed at the entrance of the burrows, are only sensitive to the movements of a strong magnetic field. Birds at Selvagem Grande mainly return to the colony to feed their chick early at night, but occasionally they arrive in late afternoon. Both parents were captured by hand as they entered the burrows. We equipped the adults of study nests with one small magnet (weighing less than 1 g), attached to a tail feather, with cloth-backed adhesive tape. Hence, animals without a magnet, such as prospecting birds occurring in the area, will not trigger the system. All 64 adult birds were ringed, and their sex was determined from calls or bill measurements (Granadeiro 1993). The polarity of the magnets deployed in males was opposite to that of females (Granadeiro et al. in press a), which enabled distinction of each member of a pair as they entered or left the nest. Males and females received a distinctive paint mark on the forehead. Occasional observations of marked animals during the night were used to validate records obtained by the automatic logger.

On 19 August, we weighed (to the nearest 1 g) and measured (to the nearest mm) the wing length of study chicks, from which we estimated their ages to the nearest two days (Granadeiro 1991). On this date, a randomly selected group of 30 chicks from an adjacent area was also weighed, and acted as a control group. Chicks in the control group were subsequently weighed on 24, 28 August and 1 September. On 22 August (hereafter designated as day 1), we began weighing study chicks at 6-hour intervals, starting at 1900 hours, following the protocol proposed by Ricklefs et al. (1985). This routine was maintained each day until the morning of 4 September (day 14). Chicks were weighed in the same order, and none of them regurgitated food during handling. The procedure took about 1 hour to complete.

Growth rates of each chick was computed as the slope of the equation obtained by regressing weight at 1900 hours each day upon date. We calculated the daily chick body condition by a common regressing of weight at 1900 hours upon

age. The residuals, expressed as proportions of the predicted values, were used as an index of body condition.

We assessed food delivery in terms of both chick feeding frequency (proportion of chicks receiving at least one feeding visit) and meal size (total amount of food received overnight by the chick). "Feed size" is used to refer to the amount of food delivered by a single parent, and nightly food delivery is defined as the average amount of food received overnight, irrespective of chicks being visited or not (zero meals included).

We estimated meal size from the sum of positive mass increments recorded between weighings (SUM, according to Ricklefs et al. 1985). This measure underestimates meal size, because it does not account for losses due to respiration and excretion. The rates of weight loss between weighings after and before a meal was delivered to chicks were linearly related to chick initial body mass and size of meal (but not age) by the following equations:

Rate of weight loss before a meal ($g.h^{-1}$) = 4.22×10^{-3} (initial weight) - 0.601

$F_{1,54} = 12.4$, $P<0.001$, $r^2 = 0.19$

Rate of weight loss after a meal ($g.h^{-1}$) = 7.27×10^{-3} (size of meal) - 2.137

$F_{1,44} = 4.5$, $P<0.05$, $r^2 = 0.34$

We corrected all nightly weight gains by the amount predicted to have been lost according to these equations, assuming that feeds occurred halfway between weighings (Bolton 1995a, Hamer & Thompson 1997).

Experimental feeding and food deprivation

Chicks were randomly assigned to each of two treatment groups. Between days 1 and 7 (hereafter designated as "control period"), we only recorded chick weight variation, as obtained from the 6-hour periodic weighing. From day 8 to the end of the study (hereafter referred to as "treatment period"), one group of chicks

(designated as "Fed") was given a daily supplemental feed, under license. The feed consisted of 30 ml of a homogenised mixture of 120 g tinned sardine in oil, with 50 ml of vegetable oil, and was administered directly into the proventriculus, using a flexible 5-mm thick catheter. The feeding procedure took about 30 seconds to complete, and none of the chicks receiving the supplement regurgitated any food. The food supplement corresponded approximately to 11 g of fat and 5 g of protein (Bolton 1995b) and represented about 40-60% of the mean nightly food delivery (Hamer & Hill 1993, Granadeiro et al. in press b). The amount of food supplemented to chicks was calculated so as to induce some improvement in body condition, without overburdening their digestive capacity (Bolton 1995b), which could affect the ability to accept more food from their parents.

In the second group of chicks (hereafter referred to as "deprived"), up to 30 g of food was removed (under license) from the proventriculus, also using a flexible catheter and a disposable syringe. The food collected consisted mainly of stomach oil, but also included a mixture of digested fish and squid. Food deprivation was undertaken each day after the morning weighings (0700 hours) and fed chicks were given the food supplement at mid-day weighing (1300 hours). During the control period, neither the periodic weighing nor the installation of the logging equipment produced any detrimental effect on the behaviour of adults (Granadeiro et al. in press b).

Chick begging behaviour

During both the control and treatment periods, we placed a small wire at the entrance of study burrows, holding closed a coil-operated switch connected to the batteries of portable audio tape recorders. As the birds entered their burrows the wire was displaced, activating the recording devices. These audio recorders were fitted with battery-amplified microphones, placed inside the burrow, and recorded the sounds produced during the following 45 minutes after activation, this limit being set by the tape length. The mechanism was installed immediately after the 1900 hour weighing, when chicks had not yet been visited by any parents. For each chick we

only recorded the begging behaviour resulting from the first feeding visit of an adult. Feeding events were easily identified by characteristic sounds, such as persistent begging calls, adult bill clapping and the clearly identifiable sound of a parent regurgitating food to the chick. Visits by prospecting birds were easily distinguished from parental visits as they were generally short and only elicited a brief (< 1 min) begging behaviour. Such visits were not recorded by the logger, and these tape recordings were excluded from the analysis. All feeding episodes recorded in this study took more than 8 minutes to complete and chick begging was continuous while receiving food (see results). We recorded the average number of calls per minute, during the first 5 minutes after the start of begging behaviour, only when there was unequivocal evidence of feeding.

Data analysis

The majority of the results presented consist of repeated observations over the same individuals. To avoid the effects of pseudoreplication, likely to occur due to the lack of independence of such data (Hurlbert 1984), all statistical tests were applied to mean values calculated for each individual chick. Throughout this paper, we present means ± standard deviation, except where otherwise stated.

RESULTS

Growth and condition of chicks

There were no significant differences among mean weights of chicks in control, fed and deprived groups, in the period prior to the start of the feeding experiment (One-way ANOVA: 19 August, $F_{2,59} = 1.8$, NS, 24 August, $F_{2,59} = 1.5$, NS; 28 August, $F_{2,59} = 2.3$, NS; Fig. 1). During the control period (day 1 to 7), fed and deprived chicks grew at a similar rate (N=32 chicks, Repeated-measures ANOVA: effect of date, $F_{6,180} = 4.1$, $P<0.001$; effect of treatment, $F_{1,30} = 0.1$, NS; interaction

effect, $F_{6, 180} = 0.4$, NS), corresponding to an average mass increase of 10.8 ± 20.7 $g.day^{-1}$ (N=32 nests).

After the onset of the treatment (days 8 to 13) the weight of chicks in the fed and deprived groups diverged (Fig.1). There was a difference between the rates of mass acquisition, indicated by a significant interaction effect between period and treatment group (Repeated-measures ANOVA, interaction effect, $F_{5,145} = 3.2$, P=0.009). There were also significant differences between days, related to chick growth, but no differences between fed and deprived chicks (Repeated-measures ANOVA: effect of day, $F_{5,145} = 20.5$, P<0.0001; effect of treatment, $F_{1,29} = 2.5$, NS).

We further examined differences in group responses by excluding the first two days after the start of the treatment (day 8 and 9), therefore allowing time for the experimental protocol to influence the condition of chicks (following Bolton 1995b and Weimerskirch et al. 1997a). Apart from the persistence of a significant between-days effect (due to chick growth), there was a significant difference between the mean weight of fed and deprived chicks and the interaction effect was no longer significant (Repeated measures ANOVA: effect of day, $F_{3,87} = 15.3$, P<0.0001; effect of treatment, $F_{1,29} = 4.4$, P=0.044; interaction effect $F_{3,87} = 0.04$, NS). The loss of a significant interaction effect indicates that both fed and deprived chicks were gaining weight at the same rate (Fig.1).

On 1 September (day 11) there was a significant difference among fed, deprived and controls mean weights (One-way ANOVA, $F_{2,59} = 3.5$, P=0.035), deprived chicks being significantly lighter than both fed and control chicks (Student-Newman-Keuls post-hoc tests).

The experimental protocol induced diverging responses of chick body condition after the start of the treatment (Table I). There were no significant differences between the average body condition of fed and deprived chicks in the control period. After the start of the treatment, fed chicks exhibited an increase in body condition (Table I).

Amount of food delivered and feeding frequency

Between day 1 and day 7, there was no significant difference between days in the proportion of nests visited (Chi-square test: $\chi^2_6 = 5.4$, NS). During this control period, fed and deprived chicks did not differ in the average nightly food delivery, meal size, feeding frequency, and size of single and double feeds (Table I). Single and double feeds recorded in this study (control period only, data from fed and deprived chicks pooled) were significantly larger than those previously reported at Selvagem by Hamer & Hill (1993)(single feeds: 73.7±26.4 g, n=236, t-test pooled variance estimates, $t_{266} = 8.0$, $P<0.0001$; double feeds: 142.6±32.8 g, n=44, t-test separate variance estimate, $t_{15} = 2.7$, $P<0.05$).

After the treatment, deprived chicks exhibited a higher average nightly food delivery and meal size in relation to fed chicks, apparently due to significant differences in the size of double meals (Table I). If the first two days after the onset of the treatment are excluded from the analysis, the average nightly provisioning rates of deprived chicks would be about twice that of fed chicks (deprived: 120.4 ± 54.5 g, N = 16; fed: 62.4 ± 42.6 g, N = 16).

Parental feeding frequencies of deprived chicks increased significantly from the control to the treatment period (Males: paired t-test, $t_{15} = 2.4$, $P<0.05$; Females: paired t-test, $t_{15} = 2.2$, $P<0.05$). Parents of fed chicks also increased their feeding frequency slightly during the treatment period, but the differences between periods were not significant (Males: paired t-test, $t_{15} = 1.8$, NS; Females: paired t-test, $t_{15} = 0.7$, NS). Despite these differences in response of parents of fed and deprived chicks, we could not find significant differences between fed and deprived feeding frequency during the treatment period (Table I).

These effects were also evident when the visiting patterns of parents were examined. The number of parental visits to deprived chicks increased significantly from the control to the treatment period, whilst visits to fed chicks did not differ between periods (Table II). However, as with the feeding frequency, direct comparison of the parental visits of deprived and fed chicks after the start of the supplementing protocol showed that these two groups did not differ significantly (chi-square test: $\chi^2_2 = 1.2$, NS).

Chick begging behaviour

Feeding episodes, defined as the time elapsed between the start of active chick begging and the end of solicitation behaviour, took between 8 and 29 minutes to complete (average = 15.6 ± 5.5 min, N=39). There was a significant reduction in begging frequency of fed chicks after the start of the supplementary feeding protocol. Deprived chicks did not alter their begging behaviour in response to the treatment (Table III). There was no significant relationship between begging frequency and either chick condition or size of meal delivered in the same or in the following night (Spearman rank correlation $r_{39} = -0.15$, $r_{39} = 0.18$ and $r_{39} = 0.12$, respectively, all NS).

DISCUSSION

In 1997, chicks at Selvagem were fed infrequently, and received meal sizes largely exceeding those previously reported in this species (e.g. Hamer & Hill 1993). Growth rates reflected this irregular feeding, being lower than that reported in other years and in other colonies (Granadeiro 1991, Klomp & Furness 1992, Hamer & Hill 1993), and especially exhibiting a high variability (coefficient of variation = 1.92). This feeding frequency resulted from the fact that parents were switching between short and long foraging trips, as found in other Procellariiformes in the southern oceans (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, 1997a, Weimerskirch 1998). On Selvagem, Cory's shearwaters delivered more food after long trips, than following short trips (Granadeiro et al in press b). By switching between these two modes of foraging, adults were able to maintain an average nightly food delivery similar to that found in other studies (e.g. Hamer & Hill 1993), and probably foraged over a more extensive area. However, this provisioning pattern implies a high variability in feeding rates, and consequently chicks were more exposed to increased risks of starvation. These observations suggest that in 1997 food availability close to the colony was below a level that would enable regular feeding visits, which appears to be the norm in this species (Hamer & Hill 1993, Mougin et al. 1996b, Granadeiro et al. in press a).

After the onset of the manipulation protocol, deprived chicks experienced a significant increase in the average nightly food delivery and consequently in the total amount of food received during parental visits, and these differences were probably related to the size of double feeds (Table I). The likely explanation for this effect is that fed chicks were rejecting part of the food brought by parents, especially during double visits (the reduction of single feeds was not significant). In fact, the average variation in the size of double feeds from the control to the treatment period was +39 g and -34.6 g for deprived and fed chicks, respectively (Table I). Given the low accuracy of the computations, these values can be considered to be relatively close to the magnitude of the treatment (± 30 g), which suggest that most of the response was accounted for by variation in size of double feeds. However, whether differences between groups in the size of feeds reflect the amount accepted by chicks, or if it corresponds to the real amount of food brought by parents could not be ascertained. We did not weight adults as they arrived to the nest, to avoid the risk of disrupting the normal feeding behaviour. Therefore, we could not assess whether adults attending deprived chicks were increasing the amount of food collected at sea, and also if parents of fed chicks were carrying smaller food loads, perhaps increasing their own body condition.

In the treatment period, the overall feeding frequency of both fed and deprived chicks was higher than in the control period, which suggest that the feeding opportunities improved during the second part of this study. This is further supported by the changes in the average nightly food delivery experienced by both fed and deprived groups. During the last four days of our study, deprived chicks were receiving an average of about 120 g from their parents, while fed chicks were receiving about half of that amount. Given that the manipulations involved the supplementation and removal of about 30 g of food respectively, the corrected nightly food delivery of both groups would be close to about 90 $g.chick^{-1}$ per day. This value is higher than the value recorded in the control period, and in fact is the highest yet reported for this species (e.g. Klomp & Furness 1992, Hamer & Hill 1993). These observations support the notion of an increase in food availability close to the colony,

from which both groups were profiting by bringing more food to chicks, thereby compensating for their former relatively poor condition.

Despite this overall increase in food availability, there was some suggestion that the magnitude of parental response of the deprived group exceeded that observed in the fed group. In fact, on a pairwise basis (control v treatment periods), the change in feeding frequency of both males and females of deprived chicks was significant, whereas that of parents of fed chicks was not (see Table II). To some extent, this argues for a compensatory response of parents to the nutritional status of their chicks in the deprived, but not on the fed chicks. This response would also explain the fact that during the last 4 days the two groups were growing at the same rate, in spite of the contrast in the treatment.

The evidences presented in this study are limited by the relatively low power of the statistical tests, arising from the small sample sizes, but mainly from the fact that the treatment was only carried out during 6 days, giving little time for the treatment to induce unequivocal responses by parents. To the extent that chicks were being visited irregularly, parents had little opportunity to assess their nutritional status and, if regulation of food delivery does occur, to develop compensatory responses. The short duration of the treatment period also precluded the assessment of changes in the relative proportion of short and long foraging trips by the adults. We would expect an increase in the proportion of short trips by adults attending deprived chicks. These trips appear to be more productive to the chick (Granadeiro et al. in press b), but probably are undertaken at the expense of adult condition.

The evidences of a possible ability of Procellariiformes to readily adjust their provisioning rate according to the nutritional status of the chicks is still equivocal. Some indication of regulation of delivery have been obtained in a few species (Bolton 1995 a, Weimerskirch et al. 1995, 1997a, Hamer & Thompson 1997), but not in many others (e.g. Ricklefs et al. 1985, Hamer & Hill 1993, Hamer 1994, Hamer et al. 1997). In these long lived species, increased provisioning effort is only likely to occur when parents do not incur increased risk of mortality (Stearns 1992, Ricklefs & Schew 1994, Weimerskirch et al. 1997a). In situations of decreased food availability, Cory's shearwater exhibit a dual foraging strategy, which probably represents a parental

mechanism to regulate the investment in offspring (Granadeiro et al in press b), as found in some Procellariiformes in the southern oceans (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1997b, Weimerskirch 1998). Therefore, if this species does have the ability to adjust their rate of provisioning according to chick needs, the effect is only likely to be clearly detected under favourable feeding conditions, i.e. when food resources are abundant and/or predictable in location, which was apparently not the case in our study.

Hamer & Hill (1994) failed to find evidence of regulation of food delivery to nestling Cory's shearwater in relation to the short-term requirements of chicks. These authors also used a supplementary feeding protocol, consisting in the daily provision of 60 g of fresh sardine fillets, and did not detect any change in the frequency of visits or in the size of meals delivered. They recorded an increase in the growth rate of supplemented chicks, in relation to a control group, but the differences in weight between groups were relatively small in the first 6 days after the start of the feeding protocol (Hamer & Hill 1994). Similarly, in our study the weight of chicks on day 11 did not differ from that of a control group (Fig. 1). These observations suggest that chicks given supplemental feeding decreased their assimilation efficiency, and possibly exhibited an increase in the excretion rates in response to the administration of the supplement. Similar abnormal reaction to supplemental feeding was recorded in Great skua Catharacta skua chicks, given a lipid/protein mixture (Hill & Hamer 1994), and Leach's storm-petrel, supplemented with a lipid-rich diet (Ricklefs 1992).

In this study, we did not consider the intensity of chick calls, but there were clear differences between chicks in begging "aggressiveness", especially during the treatment period, which could have been related to their condition. Nonetheless, there was a change in the begging frequency of fed (but not deprived) chicks after the onset of the experimental protocol, supplemented chicks exhibiting a decrease in their begging frequency. In view of the increase in the (corrected) average nightly food provisioning from the control to the treatment period, these results probably indicate a satiation effect, i.e. solicitation by chicks decreased as a response to an increase in their body condition (Table I). We could not find any evidence that begging frequency is related to the nutritional condition of chicks. A lack of relationship

between solicitation and begging in Procellariiformes had already been proposed by Ricklefs (1992). Although apparently absent in some seabird species (Ricklefs 1992, Welham & Bertram 1993, this study), the link between solicitation and parental response have been observed in other seabird species, such as Puffin Fratercula arctica and Larus gulls (e.g. Harris 1983, Impekoven 1971).

The lack of any increase in begging frequency of deprived chicks could alternatively be related to the fact that begging frequency could have been at almost its upper limit (about 1 call per 1.2 seconds). This is supported to some extent by similar data collected in Berlenga island, ca. 10 km off the Portuguese coast, where birds exhibited a high feeding frequency and were in comparatively better body condition (Granadeiro et al. in press a, b). In this island, Cory's shearwater chicks that were subjected to exactly the same manipulative protocol as that described in this paper, called less frequently (fed chicks: 28.6 ± 13.1 call.m^{-1}, N=6; deprived chicks: 40.2±11.22 call.m^{-1}, N=8; JPG unpublished data).

The paucity of information on parent-chick interactions in Procellariiformes is striking, especially in view of the fact that vocalisations clearly represent a major communication channel in this group (e.g. Bretagnolle 1989, Naugler & Smith 1992, Genevois & Bretagnolle 1994). Many species exhibit nocturnal habits ashore (Warham 1990) and vocal clues are probably more important than visual information (Bretagnolle 1989). To our knowledge, the only study examining a relationships between begging intensity and chick condition in petrels is that of Ricklefs (1992), on Leach's storm-petrel. However, the behaviour of chicks were obtained in response to handling and not under natural stimulation, and probably this behaviour does not match the normal reaction of chicks to parental presence. In fact, in chicks older than 7 days, the vocal response to handling is structurally different from the begging calls (Naugler & Smith 1992). Moreover, the frequency and intensity of calls of handled chicks appears to be mainly related to the magnitude of the disturbance, rather then to the nutritional status of the chicks (Naugler & Smith 1992). There is a clear need to further investigate whether the nutrition-dependent solicitation and solicitation-dependent foraging effort systems (Hussel 1991) occur among Procellariiformes, in

different food availability contexts, in order to ascertain the extent to which chicks are able to influence parental rates of food provisioning in this group of seabirds.

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Table 1 - Differences between fed and deprived chicks in the control and treatment periods, in chick body condition and in provisioning variables of adults. Values represent means ± standard deviation, sample size in parenthesis. Statistical testing of double feeds used only paired observations. Significant results are presented in bold.

	Control period			Treatment period		
	Deprived chicks	Fed Chicks	t-tests	Deprived Chicks	Fed Chicks	t-tests
Chick body condition	-0.021 ± 0.143 (16)	-0.013±0.094 (16)	t_{30}=0.2 NS	-0.028±0.133 (16)	0.064±0.144 (16)	**t_{30}=1.9 P<0.05**
Nightly food Provisioning (g)	62.1±25.6 (16)	59.6±16.5 (16)	t_{30}=0.3 NS	102.8±32.0 (16)	65.5 ±25.2 (16)	**t_{30}=3.7 P<0.001**
Meal size (g)	128.3±39.5 (16)	130.2±41.0 (16)	t_{30}=-0.1 NS	162.3±36.2 (16)	114.9±44.7 (16)	**t_{30}=3.3 P<0.001**
Male feeding frequency (day^{-1})	0.26±0.13 (16)	0.28±0.13 (16)	t_{30}=-0.4 NS	0.39±0.20 (16)	0.40±0.20 (16)	t_{30}=-0.1 NS
Female feeding frequency (day^{-1})	0.28±±0.15 (16)	0.29±0.20 (16)	t_{30}=-0.2 NS	0.43±0.19 (16)	0.34±0.22 (16)	t_{30}=1.2 NS
Feeding frequency at the nest (day^{-1})	0.54±0.18 (16)	0.51±0.21 (16)	t_{30}=0.4 NS	0.68±0.22 (16)	0.60±0.21 (16)	t_{30}=1.1 NS
Single feeds (g)	112.8±23.8 (16)	115.9±37.9 (16)	t_{30}=0.3 NS	119.6±40.3 (16)	99.4±38.1 (16)	t_{30}=1.5 NS
Double feeds (g)	199.6±103.1 (9)	179.5±62.8 (6)	t_{13}=0.4 NS	238.6±67.3 (14)	144.9±78.7 (11)	**t_{23}=3.2 P<0.01**

Table II - Differences in patterns of parental feeding visits of food deprived and fed chicks, between control and experimental periods.

	Food Deprived Chicks		Fed Chicks	
Number of parental visits	Control period	Treatment period	Control period	Treatment period
None	46.4%	32.3%	49.1%	39.6%
One	44.7%	45.8%	42.0%	42.7%
Two	8.9%	21.9%	8.9%	17.7%
Number of chick.nights	112	96	112	96
	$\chi^2_2 = 8.4$ P=0.015		$\chi^2_2=4.1$ NS	

Table III - Variation in begging frequency (number of calls per minute, in the first 5 minutes after feeding started) of food deprived and fed chicks. Values represent averages per chick, and statistical tests were carried out only on paired observation.

	Food deprived chicks	Fed chicks
Before treatment (days 1 to 7)	49.0±5.0 (7)	49.3±7.7 (9)
After treatment (days 8-13)	46.3±6.1 (10)	41.3±5.8 (10)
Paired t-test	$t_7 = 1.8$ NS	$t_5 = 2.6$ P=0.036

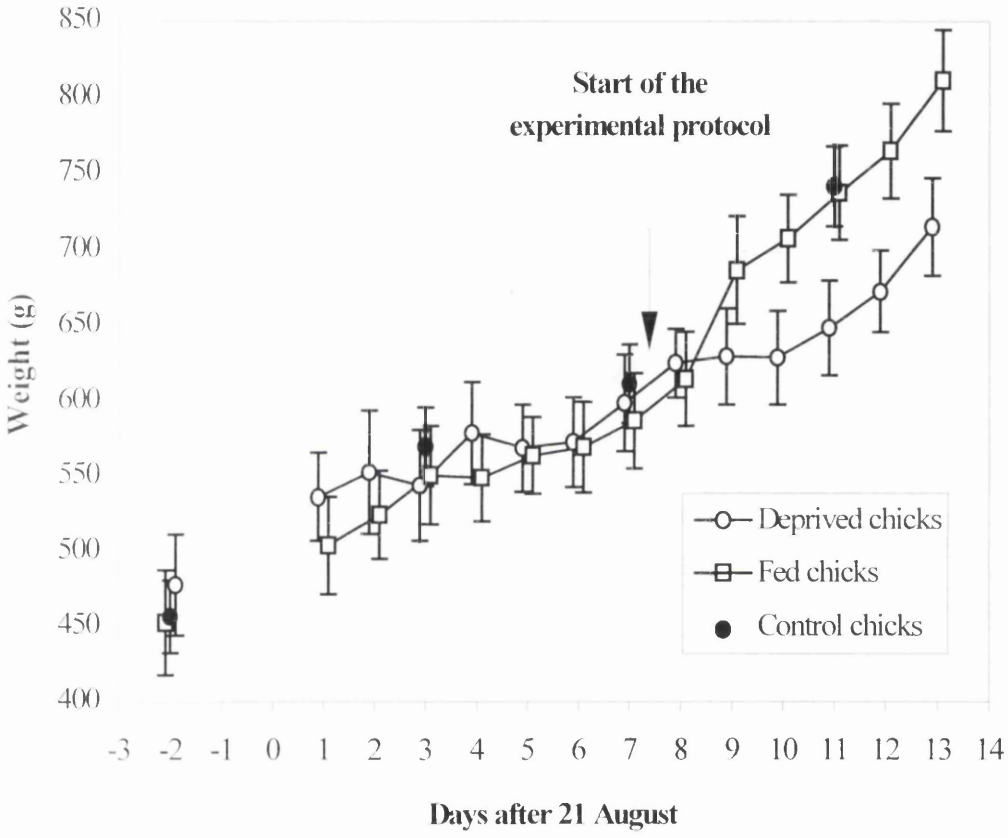

Figure 1. Weight at 1900 hours (mean ± standard error) of control (N=30), fed (N=16) and food-deprived (N=16) chicks, during the study period. Day 1 refers to 22 August.

Chapter 10

General Discussion

During the breeding season many seabird species forage over coastal waters, profiting from generally abundant food supplies in continental shelf areas (Croxall 1987, Furness & Monaghan 1987). Enhanced productivity in these areas is mainly related to continental input of nutrients, often improved by the occurrence of local oceanographic phenomena, such as coastal upwellings (Furness & Monaghan 1987).

Information on the feeding behaviour of inshore species can be obtained from direct observations at sea carried out from ships, aeroplanes and even from vantage inland locations (*e.g.* Kondeur *et al.* 1992). Most coastal species are diurnal, and so information on their foraging performance at sea can be complemented with data collected at the colonies on parental attendance, length of incubation stints, and frequency of food provision chicks at the nest. In a number of species (*e.g.* terns, auks), identification of prey given to chicks and relatively accurate estimation of their size and weight is also possible (*e.g.* Harris 1984, Frank 1992, Monaghan *et al.* 1992).

Radio-tracking have further increased the possibilities of studying the behaviour of birds while searching food at sea. Technological advances, in particular miniaturisation of components, enabled the development of minute devices, which can now be deployed in a large number of species, apparently without inducing significant changes in their foraging behaviour (Wanless *et al.* 1988, Monaghan *et al.* 1994; Calvo & Furness 1992 for a review). It is now possible to obtain accurate information on the location of feeding grounds, and under certain circumstances to obtain clues on prey catching techniques and efficiency (*e.g.* Wanless *et al.* 1993, Monaghan *et al.* 1994). The absolute performance of seabirds in finding food for themselves and for their brood can provide indications on prevailing feeding opportunities (*e.g.* Cairns 1987, 1992, Hamer *et al.* 1993, Furness & Greenwood 1993, Monaghan *et al.* 1992, 1994, Furness & Camphuysen 1997), while comparative analysis of how individual birds allocate the time between conflicting demands of reproduction and survival will convey information on their relative quality (*e.g.* Dren & Daan 1980, Lorentsen 1996, McNamara & Houston 1996).

Conversely, pelagic species forage over much wider oceanic areas, which exhibit comparatively low productivity. Procellariiformes are renowned as an extreme example of birds with a pelagic behaviour, as only a few species in this Order feed on

inshore waters (Prince & Morgan 1987, Warham 1990). Petrels do not generally visit land outside the breeding season and during the reproductive episodes, many species only come ashore during the night, presumably to avoid risks of predation (Brooke & Prince 1991, Warham 1996).

The dependence of these species on distant food resources along with their nocturnal behaviour pose major challenges to the study of their feeding behaviour (Croxall 1987, Warham 1990). Radio-tracking techniques are usually not suitable for most petrels, as they forage clearly outside the operating range of such equipment. On the other hand, direct observational procedures employed in diurnal species at their colonies are often inadequate to cope with the nocturnal and generally secretive nature of petrels. In fact, many species tend to breed in burrows (Warham 1990) and often the decision to gain access to nest chambers has to be balanced against the likelihood of nest desertion.

In the absence of data on the foraging behaviour of petrels at sea, indirect evidence obtained at the colonies has been gathered as a means to address the rules which determine foraging decisions. Dietary studies have been used to infer location of feeding grounds (*e.g.* Prince & Morgan 1987), and a large number of studies have examined the rate of energy flow to the chicks at the nests, to test hypothesis relating rates of feeding with variability in distribution and abundance of food resources at sea (*e.g.* Ricklefs *et al.* 1985, Hamer & Hill 1993). This has been done mainly by analysing variation in mass of chicks at the nests, resulting from (usually nocturnal) feeding events. To the extent that these indirect methods are usually unable to convey adequate information on the behaviour of individual parents, they are of limited use to examine the constraints that seabirds face while foraging at sea (Weimerskich *et al.* 1997a). Indeed, since foraging options are linked with condition (*e.g.* Drent & Daan 1980, McNamara & Houston 1996), allocation studies should focus on the behaviour of each parent, and this can not be resolved by examining what is experienced by the chick at the nest (Salamolard & Weimerskirch 1993, Weimerskirch *et al.* 1997a). Furthermore, males and females within a pair can differ in their level of foraging effort (Salamolard & Weimerskirch 1993), and again such differences will fail to be

detected from indirect evidences, resulting from the combined performance of both parents.

This calls for a need to improve the detail of the information which can be obtained from the analysis of chick provisioning processes. In view of the large effort and technical difficulties that the direct observation of parental behaviour would represent, the most sensible solution for acquisition of such detailed data on individual performance would involve the development of an automatic logging equipment. This would enable the collection of large amount of data over extended periods with relatively little effort, and simultaneously would avoid excessive manipulation, a pre-requisite in the study of many species, extremely sensitive to undue disturbance (*e.g.* storm-petrels). Ideally, the acquisition and archival system should incorporate facilities for frequent records of chick weight at the nest, as to enable exact assessment of size of food loads and subsequent losses due to respiration and excretion. These data should be combined with information on timing, identity and weight of visiting birds. The detection system developed in this study ensured effective acquisition of data on time and activity of visitors to the nest, and in the future this could be coupled with data obtained from electronic balances, successfully used in other seabird species (*e.g.* Sibly & McCleery 1980, Prince & Walton 1984, Gremillet *et al.* 1997).

Recently, electronic devices have started to be deployed in free-ranging procellariiformes and achieved new insights into their behaviour at sea. These include activity recorders (*e.g.* Anderson *et al.* 1991, Afanasyev & Prince 1993) and stomach temperature loggers (*e.g.* Wilson *et al.* 1992, Weimerskirch & Wilson 1992). The use of temperature loggers in albatrosses provided particularly detailed information on the amount of food eaten at different times of day. It showed that these pelagic species feed mainly during the day and extensively rely on squid species, which they mostly take as scavenged food (Weimerskirch & Wilson 1992, Croxall & Prince 1994).

However, the most outstanding results have been obtained by combining such information with data deriving from satellite tracking. This technique has enabled the acquisition of revolutionary data on the foraging behaviour and performance in Procellariiform species. For example it has revealed, as previously postulated, that

some albatrosses can forage erratically over thousands of kilometres, covering vast oceanic areas in the southern oceans (*e.g.* Jouventin & Weimerskirch 1990, Salamolard & Weimerskirch 1993, Weimerskirch *et al.* 1993, 1997b). However, the contribution of satellite tracking data extends much beyond the simple indication of location of foraging grounds, and enabled considerable insight into energy allocation processes in Procellariiformes, by identifying rules and trade-off systems through which, at least some species, appear to regulate their foraging decisions (Weimerskirch *et al.* 1997a, Weimerskirch 1998). These data have showed that during the breeding season, while tied to visit the colonies to feed the chick, some species exhibit a dual provisioning strategy, consisting of alternative short and long foraging trips (Chaurand & Weimerskich 1994, Weimerskirch *et al.* 1994, 1997b). More than simply reflecting an exchange between close and distant foraging areas, this behaviour represents a parental mechanism of reproductive effort regulation. In fact, it emerges from a trade-off system, where the chick requirements are put into balance against the need of adults to maintain their body condition above the level which would result in increased risks of mortality (Weimerskirch *et al.* 1994, Weimerskirch 1998). This implies that birds are not maximising the rate of energy acquisition and provisioning, since at some stages foraging is undertaken with net energy losses. Rather, birds are compromising energetically demanding trips on shelf areas in the vicinity of the colonies (which allow regular visits to the chick), with long trips on oceanic waters, when they rebuild their condition (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1994, 1997b). These mechanisms have only been reported in some southern ocean Procellariiformes, but there is now some evidence that this regulatory mechanism might be widespread in this group. These findings strongly support the notion that rates of provisioning in these long-living species are under the proximate control of individual parents, the regulation mechanism being probably mediated by adult body condition.

Satellite studies have mainly been restricted to albatrosses, which are large enough as to withstand the yet relatively heavy weight of the transmitters, without apparent changes in foraging behaviour. Recent trials in smaller species, such as Fulmars *Fulmarus glacialis* (Falk & Moller 1995) and Cory's shearwaters

Calonectris diomedea (Mougin & Jouanin 1997), suggest that such devices still need reduction in weight and size, as to ensure that the information collected is not biased by the effects of deployment (Calvo & Furness 1992). Nonetheless, this is clearly one of the most promising sources of information on how pelagic seabirds explore oceanic waters, and comparative data on several species, under different feeding contexts will prove crucial to our understanding of their role in marine environments.

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